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Managing Editor, RHODORA
Phippen-LaCroix Herbarium
Dept. of Biology, Tufts University
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Cover Illustration

Rhexia virginica L., meadow beauty, is found from Nova Scotia to Georgia, but is rare at the northern limits of its range. The only northern outlier of the tropical family Melastomataceae, it has distinctive 3-veined leaves and geniculate stamens. Original artwork by Josephine Ewing.

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A NEW SPECIES OF *BLEPHILIA* (LAMIACEAE) FROM NORTHERN ALABAMA

RICHARD W. SIMMERS AND ROBERT KRAL

ABSTRACT

Blephilia subnuda Simmers & Kral is described from the Cumberland Plateau province of northern Alabama. This species is compared with other species and forms of *Blephilia,* from all of which it differs in its puberulent calyx tube. From *B. ciliata* it differs primarily also in having serotinous decumbent offshoots, stems glabrate below the middle, leaves glabrate, calyx mostly shorter, and corollas paler in ground color (white to pale purple). From glabrate forms of *B. hirsuta* it differs primarily in stem vesture, leaves with fewer trichomes, calyx with longer, puberulent tube and longer teeth of lower lip, and darker nutlet color.

Key Words: *Blephilia,* new species, northern Alabama

INTRODUCTION

Blephilia Rafinesque has been considered by all recent authors to comprise two somewhat variable species, namely *B. ciliata* (L.) Benth. (*Monarda ciliata* L., Sp. Pl. 23, 1753) and *B. hirsuta* (Pursh) Benth., both confined to eastern North America. The former has its morphs most often in open areas, open woods and glades. In strong contrast is the other previously described species, *B. hirsuta,* which is primarily a mesic-woodland plant, taller (usually over 1 m), with softer, stouter stems, larger, thinner, smoother and sharper-tipped leaves, paler and softer inflorescences, shorter calyces, smaller and paler corollas and larger resin dots. The two have a broad sympatric range, namely from Vermont south to northern Georgia, west to southern Ontario, Iowa and Missouri. *Blephilia ciliata* ranges further south, into the Coastal Plain of Alabama, Mississippi, Arkansas and Oklahoma, while *B. hirsuta*

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extends further north, into Minnesota and southwestern Quebec, as well as occupying higher elevations in the southern Appalachians.

Thus we note that these two blephilias share much geographic range but overlap little in habitat; however, the two species do at times share some habitat. We have identified putative hybrids, ostensibly allowing genetic exchange by backcrossing. But even working within such a context and even when such intermediates have been identified, we have come across plants of still another and distinctive morphology that cannot be explained in terms of character states either shared or distinctive to one or the other. This taxon, discovered by the senior author in 1972 and located in the rugged, calcareous, wooded terrain of the Cumberland Plateau of northeastern Alabama, we are proposing as a new species.

Blephilia subnuda Simmers & Kral, *sp. nov.*

Haec species habitu cum *Blephilia ciliata* (L.) Benth. optime congruens sed differt stolonibus per florescentiam nullis, caulibus inferne glabratis, superne trichomatibus pro parte maxima in duobus lateribus sulcatis supra petiolos foliorum praeditis, laminis subtus glabratis, tubis calycum externe puberulis (trichomatibus usque ad 0.6 mm longis, pro parte maxima 0.03–0.10 mm longis).

Strict perennial herb (25–) 30–60 cm high, perennating by decumbent offshoots to 25 cm long, these produced only after anthesis. Sterile and fertile stems mixed in lax clusters, the stems at anthesis ca. 1–3 mm thick, the upper internodes above petioles sulcate, the branching (if present) ascending; stem surfaces commonly greenish to deep purple, glabrous or sparsely and minutely puberulent to glandular-puberulent, also with frequent tiny resin-dots from base to midstem, then from ca. midstem to tip of inflorescence, sparsely to densely mixed-trichomiferous, the trichomes spreading to recurved, even appressed, unicellular to multicellular, the longest on nodes and stem angles. Leaves spreading or slightly ascending, in the inflorescence sometimes reflexed (mostly spreading), the petioles (0.25–) 0.5–2.0 (–2.5) cm long, ciliate, puberulent; blades broadly ovate to narrowly oblong or lanciform, broadest in outline at stem base, largest at ca. midstem, progressively smaller, narrower, subsessile or sessile upstem into the inflorescence, the largest ones (2.6–) 3.6–10 (–11.9) cm long,

(0.9–) 1.2–4.0 (–5.0) cm wide; apices acute to acuminate; margins serrate to crenate-serrulate or subentire; bases round to broadly cuneate, subtruncate or attenuate, often oblique; adaxial surfaces deep green, glabrate to sparsely scabridulous; abaxial surfaces paler, glabrate or sparsely unicellular-puberulent on larger nerves; both sides moderately dotted with small, flattened, sessile glands ca. 0.08 mm wide, and puberulent to glabrate along edges. Flower clusters compact, 1–4, globose to hemispheric, 20–120-flowered, involucrate, 0.9–2.5 cm wide (at calyx level), the lower ones most distant and largest; involucral leaves green, sometimes purplish; involucral bracts numerous, loosely imbricate, the outer ones ovate to lanceolate, 7–16 mm long, 1.4–7.5 mm wide, acuminate, hirsute-ciliate, spreading in anthesis, pale green to carmine-purple, the inner ones grading to linear; pedicels 0.4–2.5 (–3.5) mm long, glabrate; calyx in anthesis slightly excurved, 5.0–8.6 mm long, the tube cylindric, slightly campanulate or flaring, (2.5–) 3.2–4.8 (–5.3) mm long, distally with a transverse hispid annulus within, externally sparsely puberulent with trichomes mostly 0.03–0.10 mm long, a few up to 0.6 mm long, sparsely glandular-punctate; upper lip 0.7–1.7 mm long, the subulate teeth 1.2–3.2 mm long, distally setose, the setae (3–) 5–10, 0.6–2.0 (–2.5) mm long, the lower lip shorter, the teeth similar but 1.3–2.8 mm long, sparsely setose; corolla externally villous, (7.5) 8.8–12.0 mm long, the upper lip linear, 1.4–1.6 mm long, the lower lip broader, longer, 3.2–5.8 mm long, 2.4–4.2 mm wide (both densely pustulate), externally white or light lilac to mauve, internally irregularly purple-maculate on the lower lip. Fertile stamens 2, the filaments 5.5–8.4 mm long, the anthers versatile, slightly exserted, rose-purple and white to light yellow, ca. 0.8–1.2 mm long, the pollen white, hexacolpate, strongly suggesting a miniature cantaloupe in form and sculpture, ca. 0.040 mm long and 0.034 mm wide. Nutlets 4, commonly ovoid, 0.7–0.9 mm long, 0.5–0.7 mm thick, uniformly black to brown-spotted or brownish, shallowly alveolate. Chromosome number unknown.

TYPE: United States. Alabama. Madison Co.: ca. 8 km NE of New Market; T1S, R3E, Sect. 18 SW¼, elev. 900–1100 ft., frequent on rich N-facing slopes over limestone, cove hardwoods S of Mountain Fork Creek, 1 June 1983, *R. W. Simmers 3423* (HOLOTYPE: GH; ISOTYPES: AUA, BH, BM, F, GH, K, MO, NCU, NY, PH, RSA, SMU, TENN, UNA, US, VDB).

ADDITIONAL SPECIMENS EXAMINED: U.S.A. Alabama. Jackson Co.: 6 mi. NW of Swain on AL HW 65, SW-facing limestone slope, cove hardwoods, 4 Jun 1975, *Massey & Whetstone 4601* (VDB); just W of dirt road along Hurricane Creek ca. 2 mi. S of Walls of Jericho, Hytop Quad., cove hardwoods over limestone, 19 May 1979, *Simmers 3256* (BH, GH, K, SMU, UNA, US, VDB); above Paint Rock Creek ca. 5 mi. N of Princeton, sandrock-boulder-strewn slopes over limestone, wooded bluffs, 7 Jun 1982, *Kral 68691* (GH, MO, NY, TENN, UNA, US, VDB); along AL 65 on NW side of Round Mt., recently logged steep, rich woods over limestone, occasional, T1S, R4E, Sect 17 NE¼, 1 Jun 1983, *Simmers 3424* (VDB). Madison Co.: Northern end of Logan Point, north of Monte Sano, alt. 430 m, 31 May 1972, *Clausen 72-16* (GH); ca. 8 km NE of New Market, T1S, R3E, Sect 18 SW¼, el. 900–1100 ft., frequent on rich N-facing slopes over limestone, cove hardwoods S of Mountain Fork Creek, 28 Jul 1972, *Simmers 2650* (GH, VDB), 17–18 May 1976, *Simmers 2963* (VDB); ca. 8 km NE of New Market, T1S, R3E, Sect 18 SW¼, frequent on alluvial terrace on S side of Mountain Fork Creek, 27 May 1978, *Simmers 3181* (AUA, BH, F, GH, K, MO, NY, PH, RSA, SMU, US, VDB); W face Huntsville Mtn., at end of Deborah St., E. side Huntsville, limerocky, hardwood-forested *Cotinus* site, 17 Jun 1983, *Kral 70174* (GH, MO, US, VDB); Green Mountain, ca. 1300 ft. a.s.l., without date, *Cindy Drake, s.n.* (VDB).

DISCUSSION

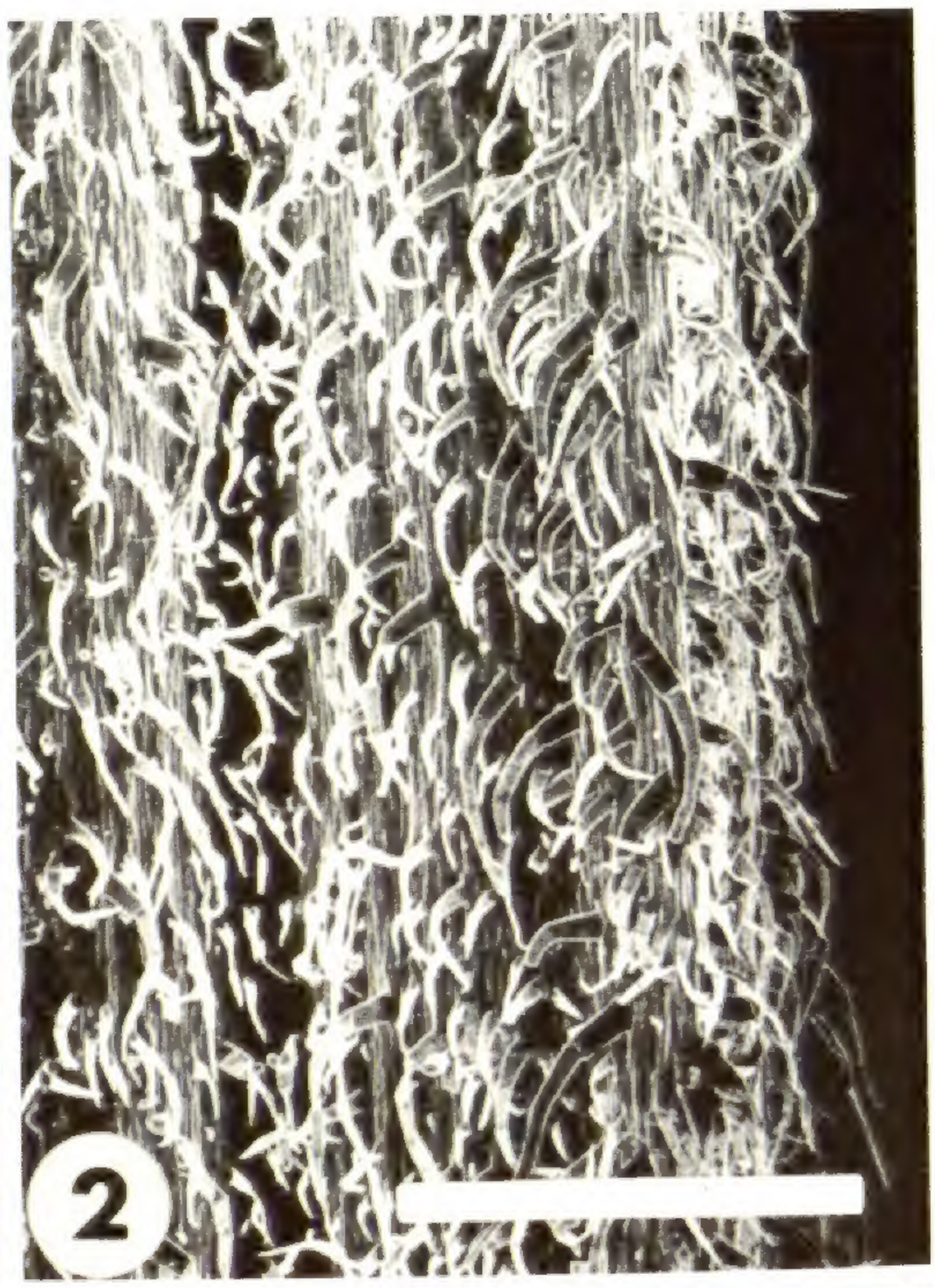
Blephilia subnuda is compared with the other two blephilias in Table 1. It stands nearest to *B. ciliata* in features of height, branching, calyx limb (relative length of teeth), bract ciliae, nutlet color and shape, and phenology. However, *B. subnuda* has longer petioles, thinner, smoother, sharper-tipped leaf blades, and smaller, paler corollas, and thus approaches *B. hirsuta* in these characters. As is true of many genera of Lamiaceae, the character and amount of vesture is given considerable weight, as are pigments. In *B. subnuda,* the most striking characters are in the smooth or virtually smooth lower and middle internodes, the smooth or nearly smooth leaf surfaces, the puberulent calyx-tube (trichomes over 0.6 mm long are lacking) and the smooth, decumbent offshoots produced after anthesis.

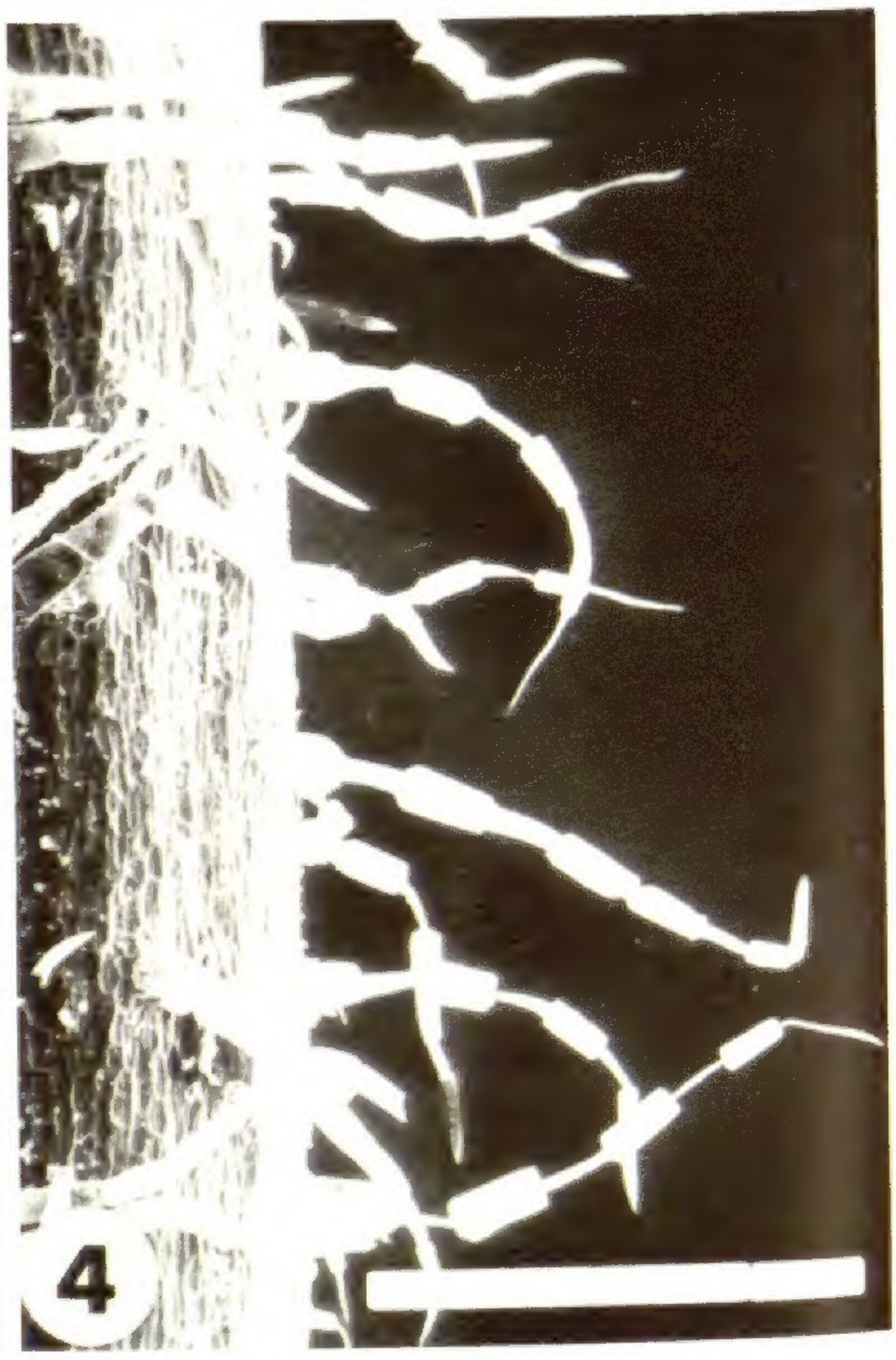
It is in degree and character of the trichomes of the stems, leaves and calyx, and to a lesser degree pigmentation, that the three species are best distinguished. Our observations are as follows:

In *Blephilia ciliata,* the most common and most variable species, the slender stems rarely range higher than 8 dm. In the sun forms (the most common situation), stems are densely pale-recurved-puberulent proximally, on most plants densely so on suprapetiolar faces. This puberulence (Figure 1) may be with or

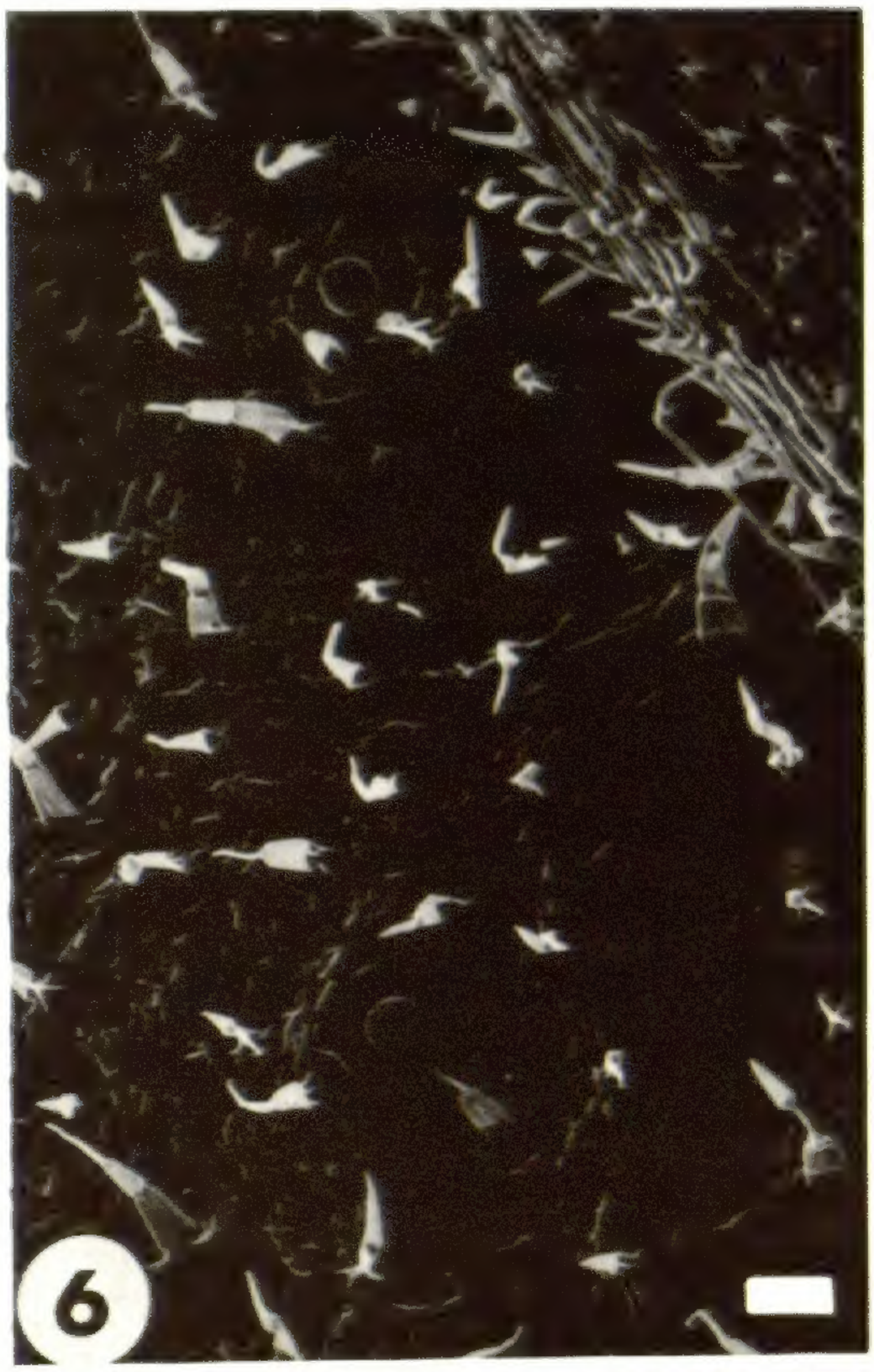
Table 1. Character states in *Blephilia* taxa.

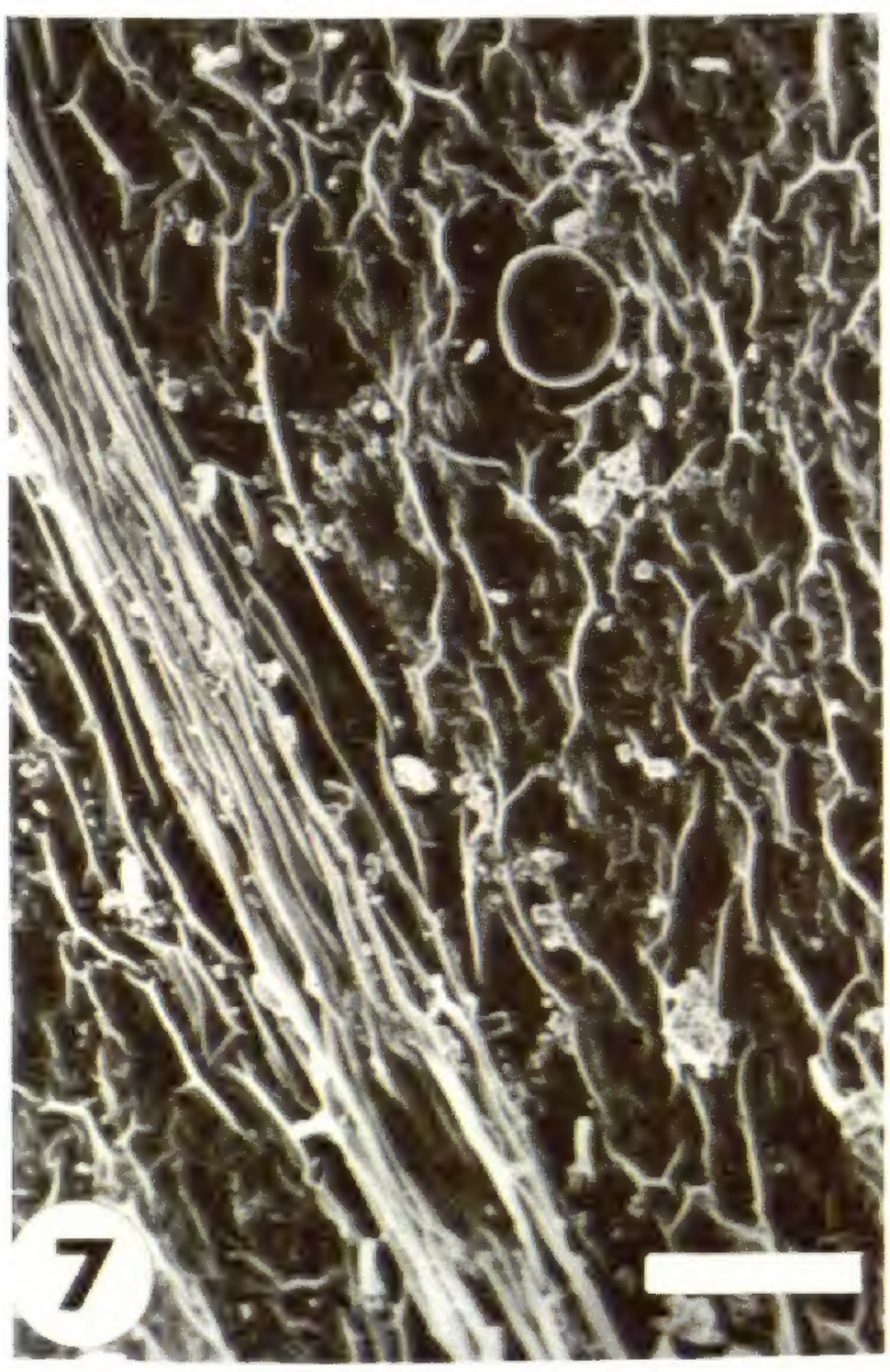
Character	*B. ciliata*	*B. subnuda*	*B. hirsuta* (typical)
Offshoots	Stolons by anthesis	Decumbent shoots after anthesis	Erect to lax shoots by autumn
Height	28–88 cm	23–56 cm	50–135 cm
Branching	Rarely, short (usually under 15 cm)	Rarely, short when present	Usually several branches over 15 cm
Stem pubescence	Dense, short, usually retrose	Glabrate below middle, ± retrorse above	Hirsute, spreading trichomes often 1–2 mm
Petiole length	1–12 mm	4–22 mm	9–42 mm
Blade shape	Oblong to elliptic to ovate	Variable, elliptic to ovate	Ovate (to lanceolate)
Apex of upper blades	Blunt	± acute	Acuminate to acute
Base of upper blades	Often cuneate	Variable, usually obtuse	Usually obtuse
Pubescence, abaxial side blades	Usually ± densely puberulent, may have some pilosity also	Glabrate, a few tiny unicellular trichomes on midvein	Pilose on larger nerves; tiny fine trichomes occasional
Calyx-tube length	4.0–8.4 mm	2.5–5.3 mm	2.2–3.6 mm
Calyx-tube pubescence	Long trichomes numerous, mostly slender, 0.6–2.4 mm	Puberulent, trichomes under 0.6 mm	Long trichomes frequent distally, ± twisted when dry
Length of upper calyx teeth	0.4–3.3 mm	1.2–3.2 mm	1.0–2.8 mm
Length of lower calyx teeth	1.2–3.5 mm	1.3–2.8 mm	0.5–1.3 mm
Corolla ground color	Shades of purple or blue	White or pale purple (lilac)	White
Time of anthesis (AL, TN)	May–June	Mid-May–Mid June	July–October (variants earlier)
Nutlet color	Black	Black, black with red-brown areas, or brown	Tan to reddish-brown

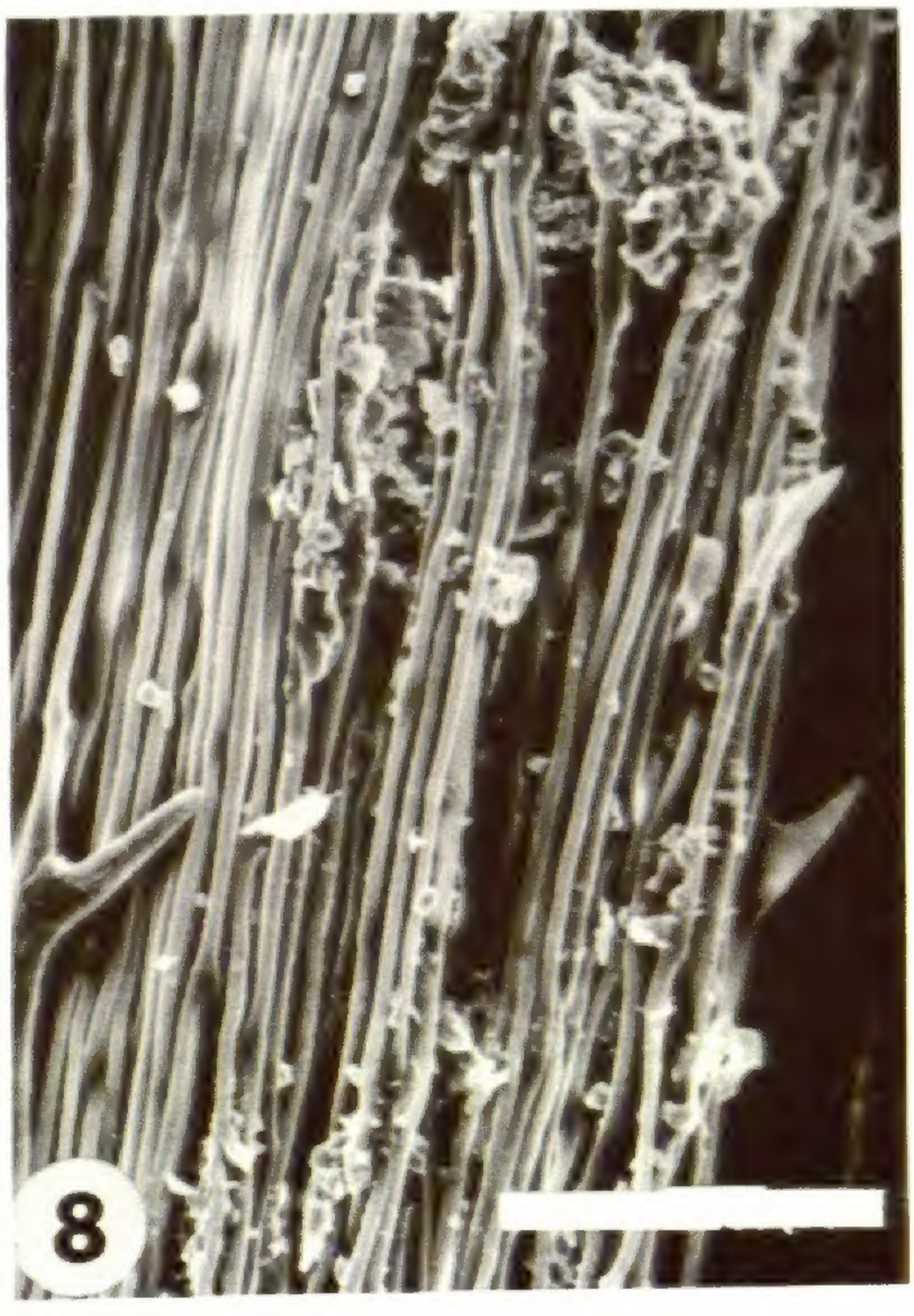




Figures 1–4. Stems (middle to upper internodes) of *Blephilia*. **1–2.** *B. ciliata* from large population near Demopolis, Marengo Co., Alabama (*Simmers 2952*); pilose extreme, plant e; usual pubescence, plant a. **3.** *B. subnuda* from type locality NE of New Market, Madison Co., Alabama (*Simmers 3181*). **4.** *B. hirsuta* from Fletcher's Hollow, Marshall Co., Alabama (*Simmers 3313*). Scale bars = 1 mm.







Figures 5–8. Undersides of cauline leaf-blades of *Blephilia*. **5.** *B. ciliata* from Highland Co., Virginia (*Simmers 3189-e*). **6.** *B. ciliata* from Tuscaloosa Co., Alabama (*Simmers 2953-e*). Figures 7–8. *B. subnuda* from type locality, Madison Co., Alabama (*Simmers 3197*). Figure **7.** Typical leaf; **8.** Maximum density of trichomes on midvein. Scale bars = 0.1 mm.

without a mingling of spreading long trichomes, particularly along stem angles, less often with such long trichomes predominant. Toward midstem a uniform puberulence may persist (Figure 2), or the vesture may consist solely of scattered or dense pilosity. Upstem, typically the pubescence becomes denser, of intermediate length, is recurved and often tomentose. The adaxial leaf blade surface is typically smoothish with scattered resin dots, the abaxial surface with short, usually soft, erect or curved puberulence, sometimes in addition with scattered pilose trichomes on the larger nerves (Figure 5). Both stems and leaves in these sun forms are generally more purple-pigmented than in the other two species. In shade forms there are extremes in which stem pubescence may be almost uniformly scattered-pilose and the thinner leaves scattered-pilose on both surfaces, rarely nearly smooth save for puberulence on the nerves beneath (Figure 6).

In typical *Blephilia hirsuta,* a strong plant usually exceeds 1 meter; the stems are thicker and softer. Stem pubescence is more uniformly long, spreading, and often villous (Figure 4); it ranges over the lower and median internodes from sparse to copious, particularly along angles and at nodes. Upstem pubescence becomes thicker and is often tomentose. In addition, the stems have frequent recurved to appressed puberulence and occasional glands. The principal leaf-blades of *B. hirsuta,* the largest in the genus, often are totally smooth between veins with scattered, often crisped pilosity confined to larger veins above (Figure 9), the sessile glands scattered, wider, more depressed, and paler. There are also occasional fine, possibly glandular trichomes present on the larger veins (Figures 9, 11), as well as puberulence. The calyx (Figures 14, 17) and involucral bracts have longer, softer, more villous pubescence than in other blephilias.

Blephilia subnuda, as noted in Table 1 and in the description, is the smoothest blephilia; the lower and often midstem internodes are totally smooth or with scattered recurved puberulence and have tiny resin-dots only. Upstem the pubescence becomes

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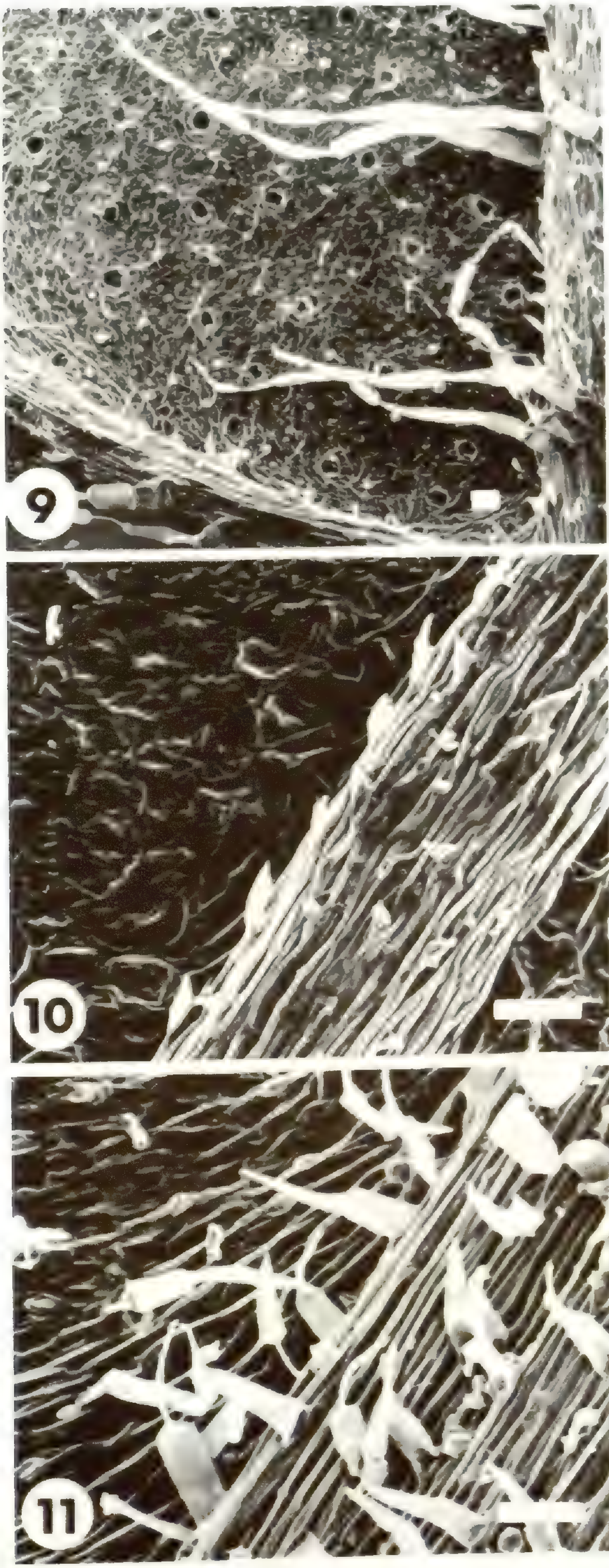
Figures 9–11. Undersides of cauline leaf blades of *B. hirsuta.* **9.** from Varna, Tompkins Co., New York (*Simmers 2992-5*). **10.** from Little River trail near Elkmont, Great Smoky Mountains National Park, Sevier Co., Tennessee (*Patrick & Simmers 3186-b*). **11.** from Fletcher's Hollow, Marshall Co., Alabama (*Simmers 3225*). Scale bars = 0.1 mm.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moderately dense on angles and faces above the petioles (Figure 3); the longer trichomes (0.5–1.5 mm long) are concentrated on the angles, the shorter ones are more numerous in the grooves. Adaxial leaf surfaces are often totally glabrous other than for glands or a few scattered trichomes on larger veins (Figure 8). The calyx tubes (Figures 13, 16) are puberulent with mainly unicellular trichomes 0.03–0.10 mm long with a few longer trichomes, especially at the orifice. The teeth of the upper calyx lip often have more numerous (5–10) setae at or close to their tips than are found in other *Blephilia.*

Occasional populations of *Blephilia,* especially in the Great Smoky Mountains of Tennessee (e.g., *Patrick & Simmers 3186*), which have stems glabrate proximally and have glabrate leaves nonetheless differ significantly from *B. subnuda,* particularly in ways that align them more with *B. hirsuta.* Such plants in summer or autumn produce strongly pubescent offshoot stems (field-checked by the senior author in November, 1979), and have a more uniform pubescence on upper parts of flowering/fruiting stems. They have relatively short petioles (3–15 mm) and the blades of upper cauline leaves are ovate to lanceolate, are acuminate with the larger nerves (midvein at least) abaxially rather densely puberulent (Figure 10), much more so than in *B. subnuda* (compare with Figure 8). Their nutlets are fuscous (dark brown), much darker than is true for typical *B. hirsuta,* in which they are tan to reddish-brown. These Smoky Mountain plants are considered here to be closest to *B. hirsuta*; possibly they have been introgressed or mixed with genes from *B. ciliata,* as is strongly suggested by the character states of petiole length, nutlet color, and relatively early phenology (often being in anthesis in June).

Fernald (*see* Day, 1899, p. 221, fn.) described *Blephilia hirsuta* var. *glabrata* from specimens collected by M. A. Day from a population on Mt. Equinox in Vermont (GH! NEBC!). Unfortunately, Fernald, who cited *Day 140 & 141,* did not indicate which of these he considered typical! The lot is variable, suggesting

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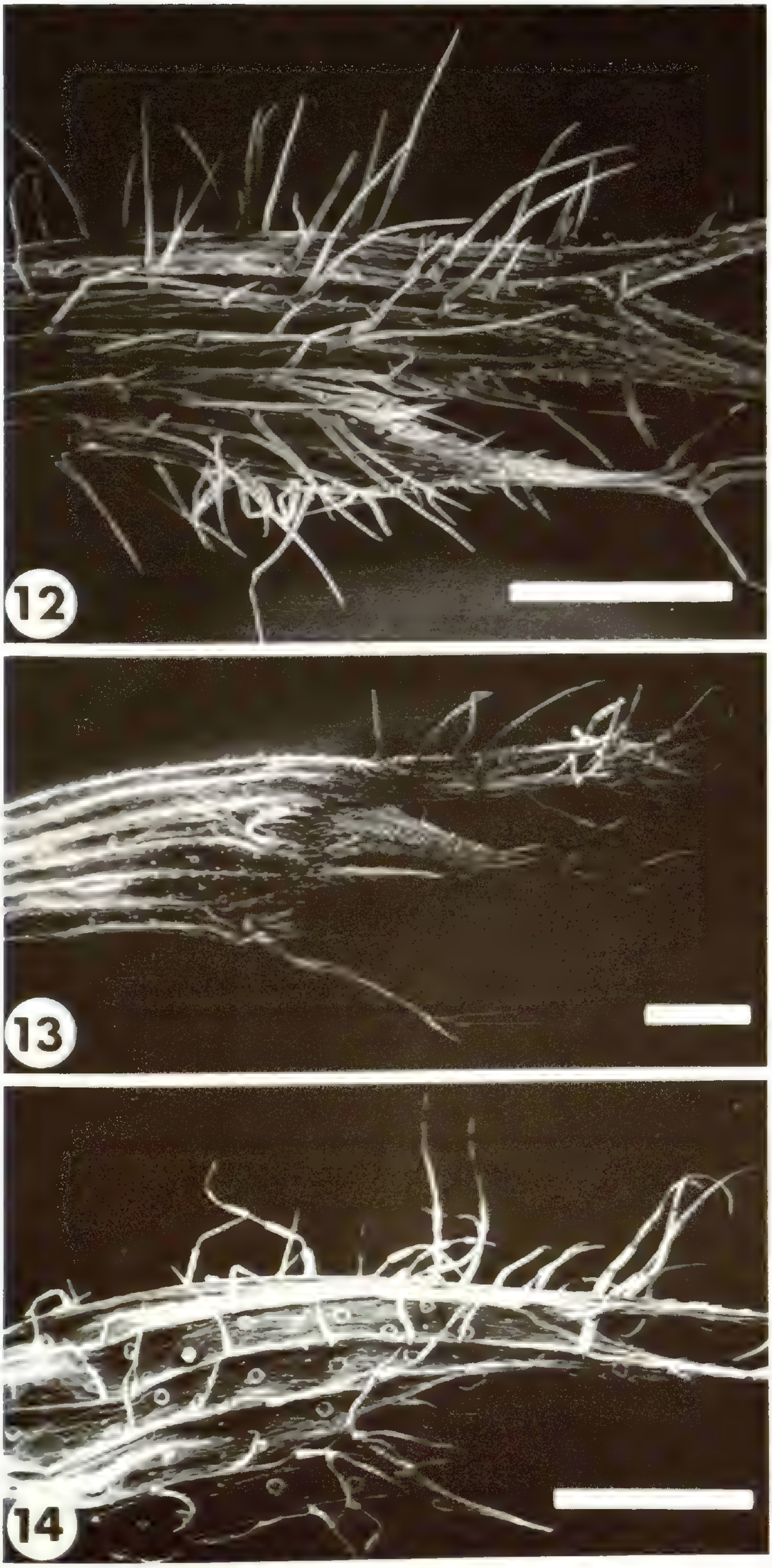
Figures 12–14. Calyces of *Blephilia.* **12.** *B. ciliata* from Tuscaloosa Co., Alabama (*Simmers 2953-e*). **13.** *B. subnuda* from type locality NE of New Market, Madison Co., Alabama (*Simmers 3181*). **14.** *B. hirsuta* from Fletcher's Hollow, Grant, Marshall Co., Alabama (*Simmers 3225-g*). Scale bars = 1 mm.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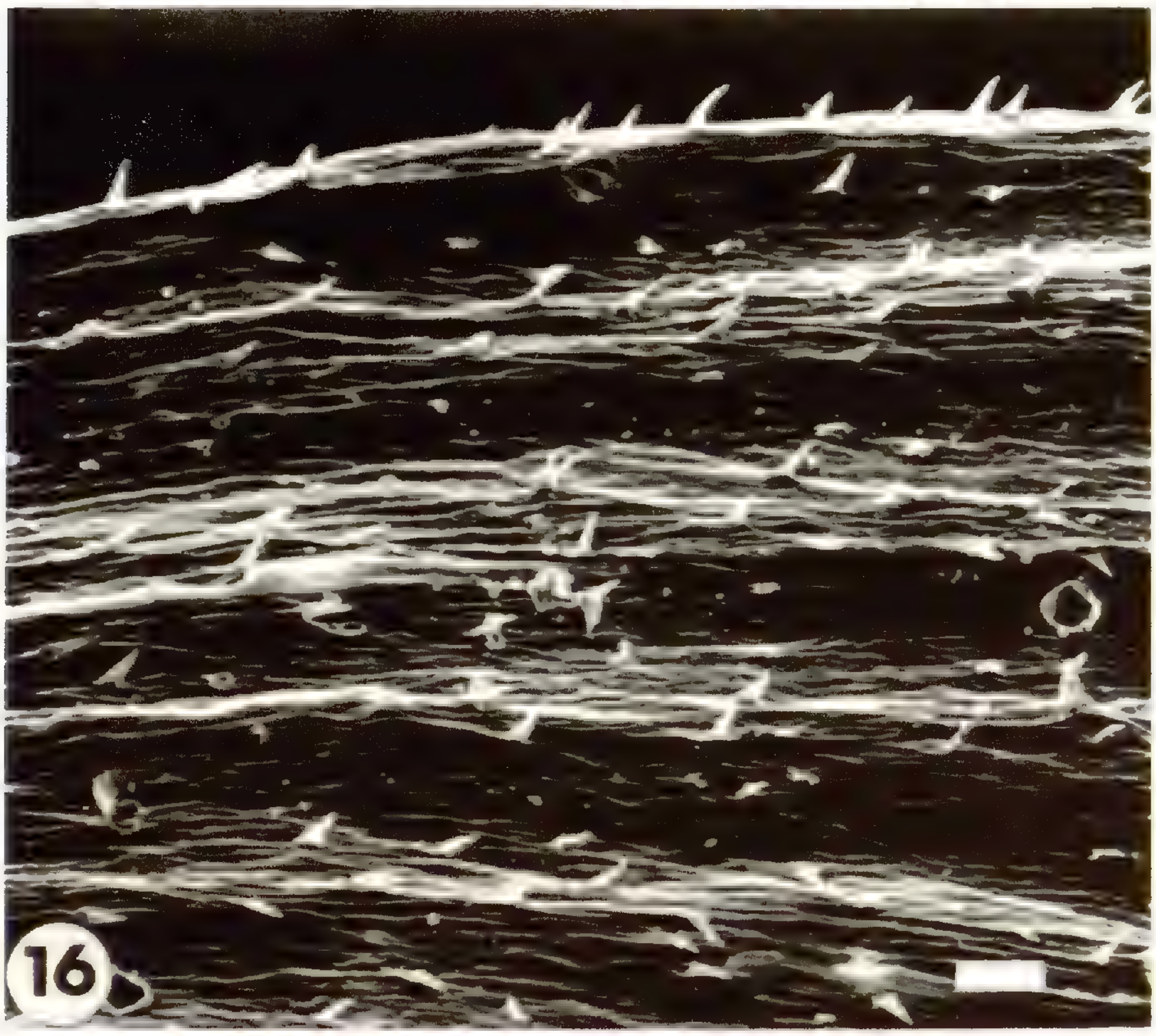
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a hybrid swarm, but none of them is much like the Alabama plants here named *B. subnuda*. One of the Day collections (*Day 141*) is nearly identical to the above-described Smoky Mountains plants, particularly as to the strongly puberulent larger nerves on its cauline leaves.

To summarize, we have a species that combines several of the salient characters of each of the two previously described *Blephilia* but which adds some distinctive features of its own, particularly a unique vesture (especially of the calyx). We consider that it is most likely that *B. subnuda* represents a stabilized hybrid. Features of vesture are an indication that selection of these characters has occurred since the initial hybridization event. A recent collection (*Simmers 1990-7*) from a population in DeKalb County, Tennessee is intermediate between *B. ciliata* and *B. hirsuta* but is unlike *B. subnuda* primarily in being densely pilose on stem and (usually) leaf; its calyx-tubes have longer trichomes than do those of *B. subnuda*. The corolla ground color of these DeKalb County plants is fairly uniformly pale violet. A few specimens close to typical *B. ciliata* have been observed and collected (*Simmers 1990-8*) on the fringe of this population, but are outside our concept of *B. subnuda*.

Blephilia subnuda has been found thus far only in two counties of northeastern Alabama north of the Tennessee River on the Mississippian limestones of the dissected Cumberland Plateau. In this region it often associates with rarities such as *Neviusia alabamensis* A. Gray and *Viburnum bracteatum* Rehder. Within its known range it is the most abundant *Blephilia*; it is locally frequent to fairly abundant, usually on shaded, moist outcrops of limestone or on slightly disturbed, fairly shaded sites including alluvial terraces. We have not found *B. ciliata* within the range of *B. subnuda*, but *B. ciliata* has been collected just outside it in Huntsville, Madison Co. (*Jada Leo, s.n.*, VDB). Populations of *Blephilia* closest to *B. hirsuta* but having reduced pubescence occur within the range of *B. subnuda* in Jackson Co., Alabama (*Kral 47572, 47574*, VDB; *Simmers 3470 & 3741*, VDB, etc.); these

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Figures 15–17. Calyces of *Blephilia*. **15.** *B. ciliata* from near Demopolis, Marengo Co., Alabama (*Simmers 3255-n*). **16.** *B. subnuda* from type locality NE of New Market, Madison Co., Alabama (*Simmers 3181*). **17.** *B. hirsuta* from Teal Hollow, Lincoln Co., Tennessee (*Simmers 3283-b*). Scale bars = 0.1 mm.

populations were not observed within 1 km of known populations of *B. subnuda*. The upland region where this endemic grows has a higher rainfall than do the surrounding areas. Therefore it is possible that the greatly reduced pubescence of *B. subnuda* is an adaptation to local environmental conditions.

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R.W.S.
8187 MACEDONIA RD.
COOKEVILLE, TN 38501

R.K.
HERBARIUM, BOX 1705, STA. B
VANDERBILT UNIVERSITY
NASHVILLE, TN 37235

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CONTRIBUTIONS TO THE ALPINE FLORA OF THE NORTHEASTERN UNITED STATES

PETER F. ZIKA[1]

ABSTRACT

Alpine and sub-alpine cliff floras have changed since botanists first explored the mountaintops of the northeastern United States; results of recent extensive field surveys are compared with the historical database to document these changes. New distribution and population data are presented for 27 rare northern taxa in Vermont, New York, New Hampshire and Maine. *Paronychia argyrocoma* is reported for the first time from Vermont. Eleven historical records for rare species are dismissed as errors. Most newly reported rare plant locations appear to be previously unexplored areas and do not represent recent dispersal. Population declines are indicated for *Arenaria rubella* in Vermont and *Luzula spicata* in New York, although the populations are in remote and pristine sites. Local extirpations are presumed in Vermont for *Arnica lanceolata, Castilleja septentrionalis, Empetrum eamesii* ssp. *atropurpureum, Geocaulon lividum,* and *Solidago cutleri,* and in New York for *Cassiope hypnoides.*

Key Words: Alpine flora, endangered species, extirpation, Maine, New Hampshire, Vermont, New York

Over the last three decades, recreational use of mountaintops in the northeast has reached all-time highs (Waterman and Waterman, 1989). Widespread soil compaction and trail erosion threatens rare members of the alpine flora. Air pollution and climatic warming are also potential threats. As a result, many alpine species are on state lists of rare, threatened or endangered plants (Countryman, 1978; Thompson, 1989; Storks and Crow, 1978; Mitchell et al., 1980; Zika, 1990a; Dibble et al., 1989, 1990). Mountain species in these references are the subject of this investigation.

The study was initiated when *Draba cana* Rydb. and *Carex atratiformis* Britt. were re-located in Smugglers Notch, after a 100-year hiatus in their collecting record. Had other high-elevation species been overlooked by recent workers? Countryman (1978) suspected the "rare" grasses of Vermont were undercollected, and this suspicion was confirmed for many species (Zika, 1990b). In this paper, for alpine and subalpine species I compare

[1] Current address: Oregon Natural Heritage Program, 1205 NW 25th, Portland, OR 97210.

some historical and contemporary data, provide evidence suggesting increases or declines in several taxa, reject eleven historical records, discuss one new state record, and record relevant population and ecological data for new stations and re-locations of some state rare, threatened or endangered species.

Distributions of most mountain species in the northeastern United States were well-known by the turn of the century (Pringle, 1876, 1897; Peck, 1899, 1900; Brainerd et al., 1900; Fernald, 1901, 1907; Kennedy, 1904; Pease, 1964). Collecting activity in alpine areas peaked between the 1870's and World War I, a period of intense professional and amateur collecting for herbaria. The results were thousands of pressed specimens and ample literature.

METHODS

Literature and herbarium searches provided a historical framework and a list of sites for intensive field surveys. Current population data were generated by repeatedly visiting classic collecting localities at Smugglers Notch (Lamoille Co., VT), Mt. Mansfield (Chittenden and Lamoille Cos., VT), Camels Hump (Chittenden and Washington Cos., VT), Mt. Pisgah (Orleans Co., VT), the Presidential Range including Mt. Washington (Coos Co., NH), and in New York's Essex Co.: Mt. Marcy, Panther Gorge, Indian Pass and Wallface Mountain. Other peaks were investigated, but less frequently. Field work was conducted between 1979 and 1990.

All species reported as locally extirpated in New York or Vermont were observed by the writer on Mt. Katahdin, Mt. Washington, or elsewhere, to learn the proper "search image," microsite requirements and associates.

RESULTS

Species are listed alphabetically; vernacular names follow Harris et al. (1964).

Agrostis mertensii

Vermont's fourth station for *Agrostis mertensii* Trin., boreal bentgrass, was recorded in 1989, on the ledgy schist summit of Mt. Hunger, Worcester, Washington Co., at 3490 feet (*Zika & Dann 10662* VT). About 20 plants were growing in turf dominated

by *Deschampsia flexuosa* (L.) Trin., with *Carex brunnescens* (Pers.) Poir. ex Lam. The colony was limited to a few square meters, and no plant was found on the adjacent exposed summit of White Rocks Mountain.

Arenaria rubella

Arenaria rubella (Wahlenb.) Sm., marble-sandwort, is known from only two locations in the eastern United States. Historical data for the Vermont population, in Smugglers Notch, include a west-side 1894 collection (NEBC, VT) labeled "rare," and an 1894 collection (VT) from north-facing cliffs in another west-side ravine, labeled "in abundance." East-side collections end in 1932 (MASS). A plant was collected on the roadside in 1926 (MASS).

Arenaria rubella can no longer be described as common or abundant in Smugglers Notch; its distribution and abundance have declined. Only two ravines currently support the species. In the last decade the population was restricted to two habitats: steep gravelly slopes, and inaccessible shelves on the tall cliffs above. The population fluctuated from 5–50. When plants were scarce most seedling establishment was observed on steep unconsolidated substrates, in mats of *Saxifraga oppositifolia* L. Following landslides, populations increase with recruitment on newly exposed gravels.

The high slopes of Smugglers Notch landslides are seldom visited by humans and are protected as part of the Mt. Mansfield State Forest. Portions are closed during the *Falco peregrinus* nesting season.

Arnica lanceolata

Arnica lanceolata Nutt., hairy arnica, is a showy subalpine and alpine species. Schweinfurth and St. John (St. John, 1987) collected it once in Vermont, in 1911, on the northern spur of Mt. Mansfield above Smugglers Notch. It has not been seen again, despite repeated searches, and is presumed extirpated in Vermont. The forested historical locality is remote and undisturbed.

In New York *A. lanceolata* shows an interesting historical distribution along the northern of the two Indian Pass Brooks. It was collected in five sites between 1899 and 1989, along 2.5 km of the stream. The population appears to episodically colonize

anorthosite shores when conditions are favorable for seed dispersal and seedling establishment. Presumably seeds are dispersed by the brook, by wind or by animals traveling along the riparian corridor.

The low elevation colonies apparently did not persist. Peck (1899) could not re-locate his original streamside station. Repeated searches in 1988 and 1989 by Steve Clemants, Rose Paul and the writer determined that the uppermost colony was the only one extant. This location was a wet exposed NE-facing cliff above the brook, and may have been a stable *Arnica* habitat and hence a reliable seed source for the lower sites, which are all forested at present. *Arnica lanceolata* (*Zika 10707* NYS) was associated with *Houstonia caerulea* L., *Thalictrum pubescens* Pursh, *Aster umbellatus* Mill., *Carex debilis* Michx., *Spiraea latifolia* (Ait.) Borkh., *Vaccinium uliginosum* L. and *Lycopodium selago* L.

One wonders what led to the loss of *Arnica* sites on Indian Pass Brook. Logging dams used 1913–1915 might have altered streambank habitats by changing the seasonality and volume of flow. *Arnica* requires openings; an important factor may have been declining light levels concomitant with shoreline forest regrowth following logging in 1913–1915. Beaver activity or siltation following logging are possible explanations; *Arnica* clones may be short-lived. Combinations of factors are possible as well.

Asplenium viride

The station of *Asplenium viride* Huds. credited to Camels Hump, Vermont "*legit* Pringle," (Brainerd et al., 1900; Eggleston, 1905; Eggleston et al., 1915) must be discounted. Pringle apparently never collected the species there, nor mentioned it in his publications. Pringle was a fern enthusiast, eagerly collecting the unusual species he discovered in the 1870's in Vermont (Anonymous, 1877; Davis, 1936). Surely he would have collected and published such a find from Camels Hump; he did so for his 1876 discovery of *Asplenium viride* at Smugglers Notch and Mt. Mansfield, as an addition to the United States flora (Pringle, 1876, 1897). There he collected considerable quantities for distribution. Pringle collected on Camels Hump only in the years 1874, 1875, and 1876 (Pringle, 1897), never returning "because its subalpine area is limited, and consequently the number of rare plants to be found there is small." No *Asplenium* was found in the course of intensive field work on Camels Hump either by the writer or by

many others, including members of the American Fern Society in 1926 (Chisolm, 1926).

No Camels Hump voucher could be found at GH, HNH, MO, NEBC, NY, SJFM, TUFT, VINS or VT. There was no reference to a Washington Co. Pringle collection in either the manuscript notes for Harry Ahles' unpublished flora of New England, nor in the Vermont checklist (Atwood et al., 1973). Those works were based on the holdings of more than 30 public and private herbaria in the region. The *Asplenium viride* citation for Camels Hump is believed to be a confusion with Pringle's record of *Woodsia glabella* on Camels Hump (Pringle 1897; Chisholm, 1926; Zika, 1982), which was not mentioned by Brainerd et al. (1900), Eggleston (1905) or Eggleston et al. (1915).

Calamagrostis pickeringii

Greene (1987) did not credit Vermont with any records of Pickering's reedgrass. Although he verified the identification of an 1877 collection from Vermont (*Pringle s.n.* US), Greene's annotation suggested the sheet was a mislabeled collection from New Hampshire, since no other collections are known from Vermont. Pringle's specimen bears no locality data besides "Vermont." It is the basis of reports in Brainerd et al. (1900), Eggleston et al. (1915), Fernald (1907, 1950) and Hitchcock and Chase (1971).

I disagree with Greene's interpretation of Pringle's Vermont record, and accept the Vermont record, as did Pringle's contemporaries. Pringle was a careful collector and there is no indication that he mislabeled other rare species he found in Vermont, the vast majority of which were confirmed by later collectors. The distribution of *Calamagrostis pickeringii* Gray in northern New York and northern New Hampshire suggests it should also be in Vermont's mountains. Its habitats and associated flora in New York (Zika and Jenkins, unpubl. data) suggest Vermont's station could have been a boggy sphagnum area on the ridgeline of Mt. Mansfield. Pringle collected heavily there in 1877.

Scrutiny of the damp mossy habitats on Mt. Mansfield's ridgeline has shown that a number of rare species have disappeared this century, including *Geocaulon lividum* (Rich.) Fern., *Goodyera repens* (L.) R. Br., *Listera cordata* (L.) R. Br., and apparently *C. pickeringii*. All the historical collection sites, in or near bogs, have been degraded by human disturbance.

Carex atratiformis

The only historical station for *Carex atratiformis* Britt., blackish sedge, in Vermont was in Smugglers Notch, where it was last collected in 1879. This population was rediscovered in 1979 (*Zika 1028* MASS, *1740* VT, *10892* VT), on both the east and west slopes of the notch, between 2200 and 3400 feet, growing with *Agrostis scabra* Willd., *Asplenium viride* Huds., *Carex leptalea* Wahl., *C. scirpoidea* Michx., *Conioselinum chinense* (L.) BSP., *Listera convallarioides* (Sw.) Nutt. ex Ell. and *Rubus pubescens* Raf.

Cassiope hypnoides

Moss plant, a circumboreal species, is at the southern limit of its range in northern New England and New York. Contrary to Mitchell (1986), Miller (1989) doubted that *Cassiope hypnoides* (L.) D. Don was ever a contemporary member of the New York flora. However, there are compelling arguments the species was present in the 1800's, suggesting it is now extirpated in New York. Two herbarium specimens (*Haberer 542* NYS, PA) and correspondence from the collector (NY State Museum botany files) are robust evidence the species was on Panther Mountain, town of Morehouse, Hamilton Co., in 1879. House (1924) confused the locality with a Panther Mountain in Essex Co., but Haberer wrote to House and emphasized *Cassiope* was in Hamilton Co.

Steve Clemants of the New York Natural Heritage Program could not find *Cassiope* in 1987 at Panther Mountain, Morehouse. As Miller (1989) pointed out, the habitat is apparently no longer suitable. The mountain is currently dominated by hemlock-hardwood forest, presumably established after logging eliminated a more boreal evergreen forest type in the 1800's. In New England *Cassiope* is an alpine snowbank species. Apparently a peripheral low-elevation habitat once existed on Panther Mountain. Partial shade from a pre-logging spruce-fir canopy may have sheltered accumulated winter snowdrifts and avalanches at the base of one of the small cliffs, forming a marginal ice cave talus community (Reschke, 1990, p. 51). *Cassiope* habitat could have been altered irreparably with logging, when the resulting second-growth was predominantly deciduous, and the crucial coniferous shade required to retard snowmelt was lost.

A second New York site for *Cassiope* was credited to C. C.

Parry in the 1840's (Peck 1891, 1900) from the summit of Mt. Marcy. Suitable habitat on Marcy's summit exists. Parry was a careful botanist who often worked in alpine areas (Britton, 1890; Parry, 1889–1897), so his report was not likely to be based on a misidentification of this unique member of the northeastern alpine flora. Miller (1989) and Adams et al. (1920) rejected the Mt. Marcy record because the voucher specimen could not be located. Certainly the missing collection creates some doubt, but fewer than 10% of the pre-1850 alpine vouchers from Vermont have survived to the present (Zika, unpubl. data); thus the Mt. Marcy *Cassiope* record cannot be summarily dismissed. Indeed, collections of the species at a lower elevation in Hamilton Co. suggest it potentially was in the High Peaks alpine zone in Essex Co. in the 1800's. Field work by Ketchledge (1984), DiNunzio (1972, unpubl. M. S. thesis, State U. of NY, Syracuse), the writer and others has failed to relocate *C. hypnoides* on Mt. Marcy. By 1880, upon failing to re-locate *Cassiope,* Peck (1891, 1900) suspected the species had already been extirpated on Mt. Marcy. I concur, and suggest the species has been extirpated in New York State.

The alpine community of Mt. Marcy was severely degraded this century by visiting hikers and campers, although the peak is currently a designated wilderness. Trampling may have affected the historical *Cassiope* location. Remote Panther Mt. remained undisturbed following logging.

Castilleja septentrionalis

Oakes (1842) reported the first Vermont collection of *Castilleja septentrionalis* Lindl. (as *Bartsia pallida* L.) by Tuckerman and Macrae in 1839, "on the north side of Mansfield Mountain, near the summit." It is not known whether this site was on the ridgetop alpine zone, or on the sub-alpine cliffs or streams in Smugglers Notch where the species is extant today, more than one-half mile northeast of (and 1500 feet below) the Mt. Mansfield ridgeline. No data are available from the label of the voucher collection; it has not been found, like most of Tuckerman's and Macrae's collections from this period. Support for an alpine rather than a sub-alpine station comes from Tuckerman's journal entries for 1839, at the Amherst College Archives. On 3 July, *Bartsia pallida* was seen on the "northeast side [of the] Chin," the summit of the alpine ridge. Further evidence is on page 88 of the same journal

for 1839. There is a list of plants found "by Edward Tuckerman junior in the alpine regions of high mountains in N. E." and it includes *Bartsia pallida* from "Mansfield mtn. Vt. 1839," and from the White Mountains in 1838.

Castilleja septentrionalis has not been found on the Chin of Mt. Mansfield since 1839. Recent intensive field searches by the writer and by Green Mountain Club rangers and caretakers (e.g., Bristow et al., 1977) indicate that pale painted cup has disappeared from this site, despite its current status as a protected natural area.

Draba cana

Draba cana Rydb. (*D. lanceolata* of northeastern authors, not Royle) was discovered in Smugglers Notch in 1878 (*Pringle s.n.* VT). Eggleston (1895) quoted Pringle's description of the population as, "a patch I could have covered with my hat." Eggleston (1895) "found a similar patch in 1893" and labeled his collections "very rare" (*Eggleston s.n.* HNH, NEBC, NY). A tiny station was documented in 1979 (*Zika 1051* MASS) at the base of an exposed xeric cliff on the west side of the notch, at 2700 feet, under a spineless *Rosa blanda* Ait., rather distant from the landslide gullies that are usually explored. The writer and David Barrington found another tiny colony in 1990 at 3000 feet, on a rotten north-facing cliff on the west side of Smugglers Notch (*Zika 10909* VT).

Draba cana is a locally common plant in Vermont only on the southwest face of Mt. Pisgah, where hundreds are extant. It was apparently first collected there in 1862 by Mann, Tuckerman, et al. (Kennedy, 1904; Fernald and Knowlton, 1905).

Empetrum eamesii ssp. **atropurpureum**

Empetrum eamesii spp. *atropurpureum* (Fern. & Wieg.) D. Love, purple crowberry, was collected on Mt. Mansfield between 1851 (*Russell s.n.* A) and 1908 (*Flynn s.n.* NEBC, VT). It has not been seen more recently, despite intensive field searches by the author and many others, and is presumed extirpated in Vermont.

Empetrum nigrum

Black crowberry, *E. nigrum* L., was discovered at a fourth station in Vermont by Harry T. Peet, Jr., in 1982. About 20 plants were located on a large schist outcrop at 3250 feet, on the south

flank of Bolton Mountain, Bolton, Chittenden Co. (*Zika, Peet & Sulek 6325* VT). It was growing with *Amelanchier bartramiana* (Tausch) Roem., *Betula papyrifera* Marsh. var. *cordifolia* (Regel) Fern., *Carex brunnescens* (Pers.) Poir. ex Lam., *C. debilis* Michx., *Cystopteris fragilis* (L.) Bernh., *Ledum groenlandicum* Oeder, *Nemopanthus mucronatus* (L.) Loesener, *Picea mariana* (Mill.) BSP., *Sorbus americana* Marsh., *Vaccinium boreale* Hall & Aalders, *V. myrtilloides* Michx., *V. uliginosum* L. and a collection tentatively identified as *V. boreale* × *uliginosum*.

Festuca brachyphylla

Festuca brachyphylla Schult. & Schult., alpine fescue, was not credited to Vermont or New York State by Frederiksen (1982) in his treatment of this arctic and western alpine species. Apparently reports of *F. saximontana* Rydb. from the northeastern United States can be referred to *F. brachyphylla*. Gleason and Cronquist (1963, p. 55) incorrectly state the habitat is "alpine summits of N. Y. and New England." *Festuca brachyphylla* is not found on summits or in alpine areas in the northeastern United States. The two historical stations in the region are Smugglers Notch and Wallface Mountain. Small extant populations were confirmed at both sites in 1990. These subalpine habitats are similar, being at ca. 3000 feet, on north-facing steep rocky turf, and partially shaded by tall cliffs. Associated species include *Campanula rotundifolia* L., *Carex scirpoidea* Michx., *Draba arabisans* Michx., *Houstonia caerulea* L. and *Saxifraga paniculata* Mill. The bluish foliage of alpine fescue helps distinguish it from similar capillary-leaved cespitose plants on the cliffs, such as sterile *Deschampsia flexuosa* (L.) Trin. and *Carex eburnea* Boott.

Some New York reports (Smith, 1965; Mitchell, 1986; Clemants, 1989) are based on a 1964 collection from Whiteface Mountain, Wilmington, Essex Co. (*Smith et al. 37420* NYS). The Whiteface specimen is *Festuca tenuifolia* Sibth.

Geocaulon lividum

Northern comandra is rare and threatened in New Hampshire (Pub. Law 93-205, Res-N 301.02), although Stern (1979) found it was widespread in the Mahoosuc Range on the Maine-New Hampshire border. Most *Geocaulon* populations in the northeast are quite small, and the distinctive rhizome is collected all too

often. *Geocaulon lividum* is a cryptic species, easily overlooked unless in fruit. In nature, *G. lividum* resembles a solitary unbranched shoot of *Comandra umbellata,* and is colored like *Vaccinium uliginosum* L., a common associate.

Geocaulon lividum was re-located in 1984 at Eggleston's 1901 station on Mt. Clinton in the Presidential Range, Bean Grant, Coos Co., N. H. (Pease, 1964). The solitary plant was observed on the edge of the Appalachian Trail at 4100 feet elev., in *Abies* scrub. To help protect the population, no voucher was collected.

In Vermont, northern comandra was known from a single site, a tiny bog on Mt. Mansfield, where it has not been found since 1901, despite intensive field searches, and is now presumed extirpated. The bogs on Mt. Mansfield have been degraded by human disturbance despite the current protected status of the alpine ridge.

Geum peckii

Only one report from Vermont was found for *Geum peckii* Pursh, mountain avens (Atwood et al., 1973). The citation was based on a collection (*Carpenter s.n.* VT) labelled: "Mt. Willoughby slope, 21 July 1926." Mt. Pisgah, on the shore of Lake Willoughby, Westmore, Orleans Co., Vermont, was often called Mt. Willoughby by collectors. There is evidence Carpenter was careless with his label data, and his Vermont record is rejected for several reasons.

No recent workers have found this endemic of New Hampshire and Nova Scotia in the Lake Willoughby area. Furthermore, Carpenter (1927) did not include the species in his article on recent additions to the Vermont flora. The date of collection also suggests a locality error. On 20 July 1926, Carpenter was collecting *Scirpus cespitosus* L. "near [the] summit, Mt. Washington, N.H." (*Carpenter s.n.* VT). It would be difficult even with modern transportation to be collecting on Mt. Pisgah one day after hiking on Mt. Washington. Why do this and then return to Mt. Washington? Carpenter was camping in the White Mountains a week later; he and Frank Dobbin saw *Geum peckii* on Mt. Washington on 29 July (Dobbin, 1927). Surely Vermont's *G. peckii* voucher is from Mt. Washington, N. H. Incongruous Carpenter labels for specimens of *Scirpus cespitosus* and *Phyllodoce caerulea* are also discussed below.

Luzula spicata

Spiked woodrush, *Luzula spicata* (L.) DC., was first found in New York by Peck in 1898, who described the station (Peck, 1900, p. 645) from the: "top of Wallface Mountain, Essex County . . . It is found in considerable abundance along the brow of the precipice that forms the western wall of Indian Pass." Spiked woodrush is no longer common on the brink of Wallface. In 1989 only 50 plants were found (*Zika 10746* NYS), in one tiny area, growing in the thin band of alpine vegetation dominated by *Deschampsia flexuosa* (L.) Trin., *Juncus trifidus* L., *Potentilla tridentata* Soland ex Ait., *Solidago spathulata* spp. *randii* (Porter) Cronq. and *Vaccinium uliginosum.* This population is threatened by trampling when rock climbers are belaying or completing their climb. A second *Luzula* population on gravelly talus directly below suggests a seed rain from the clifftop.

The lower population of *Luzula spicata* is growing in a graminoid-dominated turf among *Agropyron trachycaulon* (Link) Malte, *Agrostis scabra, Bromus ciliatus* L., *Carex debilis* Michx., *C. echinata* Murr., *C. houghtonii* Torr., *C. scirpoidea* Michx., and *Poa nemoralis* L. *Luzula spicata* is rare and very local at the cliff base, and is threatened with trampling by rock climbers. The few plants observed in 1989 were along the approach to one of more than 20 technical rock climbs on the ramparts of Wallface (Mellor, 1988).

In Smugglers Notch, Vermont, *Luzula spicata* was recorded between 1879 (*Brainerd s.n.* VT) and 1908 (*Kirk s.n.* NEBC). A small population was re-located (*Zika 10903* VT) while exploring with Cathy Paris and David Barrington in 1990, on a steep damp rocky open north-facing turf partially shaded by the steep wall of a gully on the west side of the notch.

Paronychia argyrocoma

Paronychia argyrocoma (Michx.) Nutt. (including var. *albimontana* Fern.), whitlow-wort, was not included in the flora of Vermont (Atwood et al., 1973; Seymour, 1969). Ray Angelo and the late Harry Ahles brought to my attention two Vermont specimens. One sheet has collections from several states, and several labels, one reading: "Willoughby Mt., Stowe Vt., Aug. 1865" (Ex herb. F. J. Bumstead, M. D. *s.n.* MASS). The site data on this label

are puzzling. There are several plants mounted near the label so it is not clear if the collections came from both Stowe, Lamoille Co. and Willoughby Mountain [Mt. Pisgah], Westmore, Orleans Co. Or perhaps the collections are from only one of the two label sites, and the labeler was confused or in error. The Willoughby area seems more likely. Potential *P. argyrocoma* habitat near Lake Willoughby should be explored, including a granitic cliff with *Potentilla tridentata* Soland. ex Ait. on Wheeler Mountain. This site closely resembles good *Paronychia* habitat on several New Hampshire peaks, including Mt. Willard, Crawford's Notch.

The second Vermont *Paronychia argyrocoma* collection is labeled: "rare, Vermont," with no date (*Ridler 339* BEDF). This label data is typical for a C. E. Ridler collection. His herbarium, with specimens from many states, was described by Huntington (1881) as "extensive." Ridler's vouchers include a number of rare species from cliffs by Lake Willoughby. Ridler (1884) described botanizing the cliffs above Lake Willoughby, but did not mention finding *Paronychia.* If he found the species in the area, it presumably would have been on a return trip after 1884.

There are no recent records for *Paronychia argyrocoma* from Vermont, but more field work in the Lake Willoughby region is needed to determine its current status.

Phleum alpinum

Phleum alpinum L., alpine timothy, reported from "alpine regions, Vermont, F. H. Horsford" (Dole, 1937), is not supported by an herbarium collection. The report is rejected. It is believed to be a confusion with *P. pratense* L., a weed in Vermont's alpine regions.

Phyllodoce caerulea

Vermont's only report of *Phyllodoce caerulea* (L.) Bab., mountain heath (Atwood et al., 1973) rests on a specimen labelled: "Alpine Garden, Mt. Willoughby, 5000–6000 feet, 20 July 1926" (*Carpenter s.n.* VT). Mt. Willoughby is now Mt. Pisgah (2750 feet), a peak with a "flower garden" (Kennedy, 1904). Mt. Washington, N.H. (6288 feet), has an "alpine garden." Dobbin (1927) described finding on Mt. Washington "the mountain heath, *Phyllodoce coerulea* [sic], which we had never before seen." Dobbin

was with Carpenter, and the date was nine days after the apparently mis-dated Vermont collection was made. The altitude data on the "Vermont" specimen also implies it was collected in New Hampshire. As with *Geum peckii, P. caerulea* is rejected from the flora of Vermont.

Prenanthes boottii

Prenanthes boottii (DC.) Gray, a rare northeastern endemic, is often thought to be restricted to alpine habitats (e.g., Crow, 1982). On Mt. Mansfield it was found (*Zika 4712, 4728* VT) on three schist ledges with an eastern exposure, between 3500 and 3900 feet, well below treeline, growing with *Abies balsamea, Asplenium viride* Huds., *Juncus trifidus* L., and *Lycopodium lucidulum* × *selago.* It may be in similar situations on other major peaks.

Peck (1900) discovered Boott's rattlesnake-root on Mt. Marcy in New York in 1898. He noted it was "very rare" but collected at least five plants. It is possible he overcollected and extirpated the population, as there are no subsequent records despite the intensive searches by Adams et al. (1920), DiNunzio (1972, unpubl. M. S. thesis, State Univ. of New York, Syracuse) and many others, including the writer. *P. boottii* is extant on two other Adirondack peaks. Mt. Marcy is in a designated wilderness area, but the summit has been degraded by recreational use this century.

Poa fernaldiana

Poa fernaldiana Nannf., wavy bluegrass, was last seen in Vermont in 1897. A tiny population was re-located in 1990, while botanizing with Everett J. Marshall, on the Nose of Mt. Mansfield. It was associated with *Agrostis mertensii, Carex brunnescens, Hierochloe alpina* (Sw. ex Willd.), *Lycopodium selago* and mosses, on a steep northeast slope at 3900 feet. Human disturbance in the vicinity dates back to a road and hotel constructed in 1858 at the base of the Nose (3850 feet). Communication facilities were installed on the Nose's summit (4062 feet) in 1954 (Hagerman, 1975). One unintended result was the establishment of weedy populations of *Poa compressa* L. and *P. pratensis* L. They have abrogated some alpine habitat previously available to *P. fernaldiana, Hierochloe alpina* and *Carex bigelowii* on the summit of the Nose.

Pyrola minor

Mountain pyrola, *Pyrola minor* L., is inconspicuous and cryptic. Mountain forms of the more common *P. elliptica* Nutt. often produce large mats of the reduced, rotund foliage typical of *P. minor*. At its historical site in Vermont, on the floor of Smugglers Notch near Big Spring (Eggleston, 1895), *P. minor* has not been seen since 1896, despite numerous searches, and is presumed extirpated.

A new Vermont station for *Pyrola minor* (*Zika 6211* VT) was located at 3500 feet along the Long Trail on Camels Hump, Huntington, Chittenden Co., growing with *Abies balsamea, Chelone glabra* L., *Rubus pubescens* Raf., *Solidago macrophylla* Pursh, *Thalictrum pubescens* Pursh, and *Veratrum viride* Ait. The population consisted of 73 plants in 1982. The colony, along a wet, eroding area on the footpath, is threatened by routine trail work such as ditching and waterbar installation or maintenance.

A historical population in Wilmington Notch, Essex Co., New York, was not re-located after several days of searching in 1989. More field work is required to determine its status there. However, S. J. Smith believed the colony was destroyed by altering the highway alignment in the notch in the 1970's (Alvin Breisch, pers. comm).

Salix herbacea

Salix herbacea L., dwarf willow, was reported from Camels Hump, Vermont by Carpenter (1927), Dole (1937) and Bean et al. (1956). Carpenter's original report was founded on a misidentified sheet of bearberry willow (*S. uva-ursi*) at the Pringle Herbarium (Kirk, 1950). *Salix herbacea* is rejected from the Vermont flora.

Salix planifolia

Tea-leaved willow, *Salix planifolia* Pursh, is an alpine and subalpine species in the northeastern United States. Seymour's (1969, 1982) habitat summary: "meadows, swamps" is incorrect for our area, implying low elevation habitats. The statement appears to be based on records from other parts of the species' range, or on misidentified specimens of *Salix discolor* Muhl. from low ele-

vation sites. Four such records are discarded: Vermont collections from Burlington, Fairfax, Stratton and Westford, cited in 1973 by Atwood et al. Vermont's only station for *S. planifolia* is on Mt. Mansfield, and it is extant where Pringle discovered it in 1877.

Scirpus cespitosus

Random extinctions are predicted on functional islands of alpine habitat by island biogeographic theory (MacArthur and Wilson, 1967). This assumption probably explains how deer's hair can be locally dominant in the alpine zone in New Hampshire and New York, yet absent in appropriate habitat in the alpine zones of Mt. Mansfield and Camels Hump. *Scirpus cespitosus* L. is present on the west slope of Mt. Mansfield on sub-alpine ledges at 3000 feet (*Zika 724* VT). It is a dominant on the northeast side of Mt. Mansfield, in Smugglers Notch, where it occurs with many of the species found in the Willoughby flora. The current distribution of *S. cespitosus* suggests it may have been present on the summit of Mt. Mansfield, and became locally extinct prior to the first botanical investigations. Examination of macrofossils from the bogs on Mt. Mansfield could answer this question.

Scirpus cespitosus is absent on the sub-alpine cliffs of five peaks around Lake Willoughby in Westmore, Orleans Co., Vermont. A solitary Mt. Pisgah record (*Carpenter s.n.* VT) from 21 July 1926 appears to be one of several mis-labeled alpine Mt. Washington records (see *Geum peckii* and *Phyllodoce caerulea*), and is dismissed.

Solidago cutleri

Solidago cutleri Fern., alpine goldenrod, is endemic to the mountains of northern New York, Vermont, New Hampshire and Maine. On some ranges it is a common component of the alpine community. In Vermont the population in Smugglers Notch was last documented in 1891. A tiny population was re-located in 1990 on a schist shelf in a ravine on the west side of the notch, at an elevation of 3000 feet. It was growing with *S. spathulata* ssp. *randii,* which is common in the area. The presence of suspected hybrids and the extreme rarity of *S. cutleri* suggests that genetic swamping may be a problem for this population.

The population of alpine goldenrod on the Chin of Mt. Mansfield has not been documented after 1908 (*Flynn s.n.* VT), and is presumed extirpated. It seems unlikely this bright-flowered species could be overlooked during the intensive searches conducted by the author, Bristow et al. (1977) and others. The Chin has been heavily trampled along hiking trails, but is otherwise little changed from the turn of the century. Botanical collecting may have been important in the decline of this population.

Streptopus xoreopolus

Streptopus xoreopolus Fern., mountain twisted stalk, was considered "possibly extirpated" in Maine (Dibble et al., 1989) and was not seen in searches in 1988 (Dibble et al., 1990). A small population was located in 1990 on Hamlin Peak, T3, R9, Piscataquis Co. Five flowering plants were in a snowbank community at the base of an an alpine cliff with northeast exposure at 4650 feet elevation, growing with *S. roseus* Michx. and *S. amplexifolius* (L.) DC. The hybrids displayed the strongly clasping leaves and habit of *S. amplexifolius,* combined with the hispid herbage and pink flowers typical in *S. roseus.* Associates included *Cassiope hypnoides, Gaultheria hispidula, Loiseleuria procumbens* (L.) Desv., *Luzula parviflora, Maianthemum canadense, Phyllodoce caerulea, Poa fernaldiana, Rubus pubescens,* and *Vaccinium cespitosum.* To help preserve the colony, no voucher was collected.

Vaccinium cespitosum

Vaccinium cespitosum Michx., dwarf bilberry, is unique among the mountain *Vaccinium* species, with its serrated obovate leaves and solitary axillary flowers. It is probably overlooked because it is low and inconspicuous, and may be more common in river gorges in the northeast than the limited number of current records indicate; Jenkins and Zika (1987) found it on the Missisquoi, Wells and West River drainages in Vermont. The species is scarce but extant at several locations along the ridgeline of Mt. Mansfield, from near the Octagon to the Adams Apple, between 3650 and 4370 feet. In New York a new station was observed along the trail between Lake Tear of the Clouds (4300 feet) and the Panther Gorge shelter (3250 feet), southeast of Mt. Marcy, Keene, Essex Co. Another new population was observed on wet ground

along the trail on the southeast shoulder of Mt. Haystack, Keene, at 3750 feet. About 700 plants were seen on the northeast slope of Mt. Marcy, where it is common between 4800 and 5200 feet in sheltered alpine areas, near treeline, in the general area where Peck (1900) reported it.

Viburnum edule

Squashberry, *Viburnum edule* (Michx.) Raf., often occurs in small populations of 1–6 shrubs in the northern Appalachians. A number of colonies are sure to remain undocumented until there is more off-trail exploration of the headwaters of small mountain brooks, a favored habitat for the species. *Viburnum edule* is extant at four locations on the ridgeline of Mt. Mansfield, Vermont, between 3500 and 3900 feet, growing with *Salix planifolia* and other shrubs (*Zika 4714, 4715, 4719* VT). The Mansfield population extends into the towns of Cambridge and Stowe, Lamoille Co., as well as into Underhill, Chittenden Co. A new Vermont locality is on the trail to the abandoned fire tower on Mt. Monadnock's east slope, at 3000 feet, in Lemington, Essex Co. (*Zika 9217* VT). Another new station is on Camels Hump, at 3500 feet in Huntington, Chittenden Co. Nine shrubs were found in wet thickets (*Zika 6212* VT).

In New York, new locations of small populations were sighted in 1989 on Santanoni Brook (Newcomb), and Algonquin Peak (Keene, *Zika 10685* NYS). One colony was seen on Phelps Brook (North Elba) in 1981 (*Zika 5077* VT). Extensive colonies (10–100 shrubs) were seen along the northern Marcy Brook at Indian Falls (Keene, Zika 1981 and 1989 observations), on Opalescent River below Uphill Leanto (Keene), on two small brooks draining northeast and southwest of Lake Arnold (Keene), and on the southern Marcy Brook that drains Panther George (Keene). All these sites are in Essex Co., in the Adirondack Mountains.

DISCUSSION

How recently established are these newly reported montane stations? Why were the localities not documented in the herbaria of the numerous, and apparently quite thorough, collectors of the last century? Has there been a recent widespread dispersal of these rare taxa? This last possibility is doubtful. Consider six rare moun-

tain taxa in close proximity in the Adirondacks: *Epilobium hornemannii* Reichenb., *Festuca brachyphylla, Loiseleuria procumbens, Luzula spicata, Poa fernaldiana,* and *Salix herbacea.* Historically, each is documented from a single site. If they suddenly appeared on a second peak it would suggest recent dispersal, which simply has not happened.

A more likely, though speculative, explanation is that "new" populations of *Prenanthes boottii, Agrostis mertensii, Empetrum nigrum* etc. are apparently relictual early Holocene populations overlooked or inaccessible to previous botanists. Three Vermont examples, from Mt. Mansfield, Bolton Mtn., and Camels Hump, are given as circumstantial evidence to illustrate the point.

Bear Pond, which is not visible from the alpine ridge, was not mentioned on any of the ca. 1200 herbarium labels I examined for Mt. Mansfield. Bear Pond populations of *Asplenium viride, Carex atratiformis, Prenanthes boottii,* and *Viburnum edule* were apparently ignored by earlier botanists who collected these species from more accessible areas. Harold St. John (pers. comm.) bushwhacked through formidable krummholz in this area in July 1911 because it was still trailless; he and earlier botanists could easily have missed the ledges with rare species in such difficult terrain. A modern trail now provides access to the vicinity.

Empetrum nigrum and its alpine associates on a Bolton Mountain cliff were discovered in a remote trailless area only when scouting for a new route for the Long Trail in 1982 (Peet, pers. comm.).

On Camels Hump, the dismantling of overnight huts in the hut clearing (3800 feet) and the construction of Gorham Lodge 0.4 miles to the north (3400 feet) was not done until 1950 (Peet, 1977). Thus only recently has there been convenient lodging north of the hut clearing. Naturally the botanical work of the last century focused on the alpine regions south of the hut clearing, and not on the low diversity boreal forest to the north, where a trail was not built until 1910–1911 (Waterman and Waterman, 1989, p. 358). Day hiking trails used by Robbins, Macrae and Tuckerman (Oakes, 1842) were from the east or west, as today. Longer (overnight) hikes from the north apparently were avoided by botanists; e.g., Chisolm (1926) reported a botanical field trip climbing from the east, not the north. "New" sites for *Pyrola minor* and *Viburnum edule* in this paper are on the north trail.

Viburnum edule, and to a lesser degree *Vaccinium cespitosum,*

are the only species studied with substantial numbers of newly reported stations. These sub-alpine (to low elevation) species were largely found in areas accessible to modern botanists due to recently constructed hiking trails and roads. More sites should be found with the off-trail exploration of mountain headwater brooks (*Viburnum edule*) and boating in rapids and river gorges (*Vaccinium cespitosum*).

It is becoming clear that the floras on our alpine peaks are changing; the data show several species declined or became extirpated from alpine areas this century. The reasons for this change are not clear, but several possibilities can be offered. Effects of human disturbance, generally associated with recreation and botanical collecting, may have been detrimental in the past. The Little Ice Age ended in the early 1800's (Dansgaard et al., 1975); Hamburg and Cogbill (1988) noted an average summer temperature increase of more than 2°C at stations in Massachusetts and New Hampshire since 1830. Climatic amelioration following the Little Ice Age could have a negative impact on disjunct species in alpine areas. If so, then current predictions of increased global warming may have serious consequences in the plant communities in northeastern alpine areas. Chronic pollution may also be a potential threat in the future.

Further studies of historical extinctions of alpine species are needed in alpine areas across the northeast (e.g., Dibble et al., 1990). Demographic studies are needed for the apparently declining populations of *Arnica lanceolata, Arenaria rubella,* and *Luzula spicata* in order to determine the proximate and ultimate causes of population shifts; all are in remote, protected areas, and the latter two are in essentially pristine habitats. They may be bellwether species for the boreal flora of the northeast.

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NEW YORK NATURAL HERITAGE PROGRAM
WILDLIFE RESOURCES CENTER
700 TROY-SCHENECTADY ROAD
LATHAM, NY 12110

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A NEW FORM OF *TRIPHORA TRIANTHOPHORA* (SWARTZ) RYDBERG, AND PART 3 OF OBSERVATIONS ON THE ECOLOGY OF *TRIPHORA TRIANTHOPHORA* (ORCHIDACEAE) IN NEW HAMPSHIRE

PHILIP E. KEENAN

ABSTRACT

An albino form of *Triphora trianthophora* (Swartz) Rydberg is described as forma *albidoflava* Keenan, characterized by pure white sepals and petals, and the three crests on the lip petal being a bright yellow instead of the normal green color, the remainder of the plant creamy-white. A summary of conclusions on observations of the three-birds orchid in Holderness, N.H. at two different sites, one under study for twenty years, the other for six years, including these: approximately five or six days of flowering spaced over a bloom period from the first week in August to the first week in September; variation in population from a few thousand to several thousand each year; simultaneous blooming in a region encompassing New Hampshire, Maine and Massachusetts; more than 95% of the plants having either one or two flowers open at the same time.

Key Words: *Triphora trianthophora*, albino color-form, ecology, New Hampshire

Triphora trianthophora (Swartz) Rydberg f. *trianthophora* is characterized by a mostly white flower with varying degrees of purplish-pink suffusion around the edges and at the tips of both sepals and petals. The lip petal is highlighted by three parallel ridges of teeth-like projections, bright green in color.

Field work in the Holderness, N.H. area in October 1987 yielded my first albino plant, with mature upright fruit in the dehiscent stage. In August, 1990, I discovered my first albino plant in flower in the same general area, but not the same plant found in 1987. This site has been under my surveillance every year for six years and is the largest station I have ever seen or known about both in terms of area covered and total population. The site measures approximately one quarter mile in length and one hundred feet in width, while the population has varied from approximately two thousand plants to more than ten thousand, depending on the year.

The single albino plant had four buds. The stem and leaves were a creamy-white color. The very base of the stem had a bit of purplish suffusion. The sepals and petals were white without a trace of purple. The characteristic green coloring of the lip petal's

three ridges was replaced with a pure yellow color. The pollinia retained their purplish color.

Triphora trianthophora (Swartz) Rydberg forma **albidoflava** Keenan

Differt a forma *trianthophora* caule foliisque sine ullo pigmento viridi, sepalis petalisque sine ullo pigmento purpureo, crista triplici omnino flava sine ullo pigmento viridi in labio.

Differing from forma *trianthophora* in its stem and leaves lacking all green pigment; the sepals and petals lacking all traces of purplish pigment; the triple crest without any green pigment on the lip, the green replaced by pure yellow.

TYPE LOCALITY. United States. New Hampshire, Grafton County: Open, deciduous beech forest. August 10, 1990. (HOLOTYPE: NHA, color photographs.)

ETYMOLOGY. From albido, white and flava, yellow, referring to the yellow crest on the otherwise white lip.

I am indebted to Paul Martin Brown of the New England Wild Flower Society, and Dr. Leslie Garay of the Oakes Ames Herbarium at Harvard for their help in checking the authenticity of this new taxon.

The discovery of this new color form culminates almost twenty years of nearly annual visits to two stations of *Triphora trianthophora* in Holderness, N.H. (Keenan, 1986, 1990a). The August, 1990 season was one of the more remarkable. Among the interesting surprises was the discovery of one exceptionally large clump, which contained, by individual count, approximately 750 stems, packed tightly together in the extremely small area of 15 × 25 cm, the majority of them blooming en masse on August 10th. This massive bloom was very impressive; it was illustrated in part in Keenan, 1990b, which see. Case (1987) attributed these larger clumps to squirrel caches, with corms piled in several layers; I am not convinced by this explanation, however.

The second most interesting happening in 1990 was the flowering—and non-flowering—of a single four-bud albino specimen described at the beginning of this article. Color photographs of

this new taxon also appear in the American Orchid Society Bulletin (Keenan, 1990b).

The albino plant produced its first open flower on August 10th. That event left three other tight buds, two which were large and a week away from opening, and the much smaller third one two weeks from opening.

On the 18th of August there occurred the third major mass blooming of the 1990 season. On that day, the two large albino buds should have opened but did not. Consequently, I drove up to Holderness again the next day, Sunday, again to no avail. I continued to visit the site each successive day determined to catch the two large buds when they finally opened. Wednesday, the 22nd, four days after they should have opened, the two larger buds, for the first time, changed color from the pure white of the preceding days to a dull, almost sickly, pale cream. This change indicated to me that they would not open. Meanwhile, the tiny third bud continued to enlarge each day and now was erect and white, sure to open the next day, which it did, on Thursday, August 23rd. On this same day, the two large buds dropped off the plant, as I expected they might do in view of their color change the previous day. The question of why these two buds failed to open on the day they could be expected to, then deteriorated and dropped off without opening at all, is a very perplexing one to me. As noted, the first and last of the four buds did open, despite the fact the last bud was much smaller than usual, and smallest of the four. The albino plant measured 120 mm tall; the tiny fourth flower only 10 mm long and 13 mm wide when fully open.

The 1990 season was an excellent one for *Triphora* in the Squam Lake region over and above the two remarkable phenomena detailed above. There was a total of five bloom days for the month of August, i.e., only five days out of thirty-one had open flowers. Three of these days, August 3rd, 10th, and 18th, were days of major blooms.

Herewith I present a summary of conclusions based on these two Holderness, N.H. stations during my twenty years of observations:

1. Flowering period occurs from the first week in August to the first week in September.

2. Only five or six days in the entire monthly period have open flowers.

3. Flowers are fully open for that one calendar day. Rarely,

during cooler temperatures, will flowers remain approximately one-quarter open the next day.

4. Contrary to Morris and Eames (1929) contention, plants do not have "one flower partly open, one flower fully open, and one flower partly closed" on the day a flowering takes place.

5. Less than approximately 5% of plants have 3 flowers open at the same time. Approximately 95% of plants have either one or two flowers open at the same time.

6. Open flowers occur simultaneously on the same day throughout the region of New Hampshire, Maine (fieldwork with Les Eastman of the Josselyn Society), and Massachusetts (personal communication, Sue Williams, studying a *Triphora* population in western Massachusetts for the Natural Heritage Inventory of the State of Massachusetts).

7. All buds open by 10 a.m. (my earliest arrival time) but probably sooner, on the day a flowering occurs.

8. Every year above-ground plants are produced; these plants vary in number from several hundred to several thousand, with approximately all plants producing at least one bud regardless of the size of the plant.

9. Judgment on population numbers should be based on observation early in August because of potential rodent destruction later in the month (Keenan, 1986).

10. Judgment on bud numbers must be ascertained early, before first bloom, because many closed flowers drop off the plants quickly if not fertilized.

11. Relatively small percentage of flowers produce mature fruit.

12. Nearly 100% of plants grow in beech leaf litter. This environment can be in the typical beech-forest shallow depressions or just as often on flat ground with thin accumulations of beech leaves, or in decomposing log material beside fallen logs, but almost never directly on top of rotting logs.

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31 HILLCREST DR.
DOVER, NH 03820

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NOMENCLATURAL NOTES ON NORTH AMERICAN *HYPOXIS* (HYPOXIDACEAE)

ALAN HERNDON

ABSTRACT

The name *H. micrantha* Pollard is shown to be currently misapplied; plants going under that name in recent floristic treatments are referable to *H. wrightii* (Baker) Brackett while *H. micrantha* Pollard is properly regarded as a synonym of *H. hirsuta* (Linnaeus) Coville. *H. curtissii* Rose is shown to have priority over *H. leptocarpa* (Engelmann & Gray) Small. Lectotypes are selected for *H. rigida* Chapman and *H. sessilis* Linnaeus.

Key Words: *Hypoxis*, North America

INTRODUCTION

The following notes are intended to justify the application of certain names and other nomenclatural details in the updating of *Hypoxis* for the Flora of North America. This floristic treatment will appear prior to completion of a formal revision of the North American species.

Hypoxis micrantha Pollard in Small, Flora of the Southeastern United States: 287, 1392. 1903. TYPE: North Carolina, Cartert Co., 19 July, *G. McCarty 8* (HOLOTYPE: US *245935*!)

Two sheets at US bear notations in what appears to be Pollard's handwriting which identify them as types of *Hypoxis micrantha* Pollard. Only one of these sheets (*McCarty 8*) was cited in the original description and, accordingly, must be treated as the holotype. This sheet contains a few plants of what I consider to be depauperate *H. hirsuta*. The second sheet contains plants of three different species: *H. wrightii* (Baker) Brackett, *H. leptocarpa* (Engelmann & Gray) Small, and depauperate *H. hirsuta* (Linnaeus) Coville. Brackett chose an element representing *H. wrightii* as the exemplar for the name and based her concept of the species on this. Since this attribution is contrary to an existing holotype, it must be ignored. I find no taxonomically significant difference between *H. micrantha* Pollard and *H. hirsuta* (Linnaeus) Coville.

Hypoxis wrightii (Baker) Brackett, Rhodora 25: 140. 1923.

Hypoxis juncea var. *wrightii* Baker, J. Linn. Soc., Bot. 17: 106. 1878. TYPE: CUBA, 1865, *C. Wright 239* (HOLOTYPE: K!)

Hypoxis wrightii is the correct name for the Atlantic Coastal Plain species called '*Hypoxis micrantha*' in recent floristic treatments. Current misuse of the name *Hypoxis micrantha* is due to Brackett's (1923) misunderstanding of the type outlined above. The species called '*Hypoxis micrantha*' in Brackett (1923) is presumably differentiated from *H. wrightii* (Baker) Brackett on the basis of seed coat color and sculpture, '*H. micrantha*' having a brown, finely muricate seed coat and *H. wrightii* having a black, coarsely muricate seed coat. There are discrepancies in her revision with regard to these characters. In the key, both '*H. micrantha*' and *H. wrightii* are treated under mature seed brown or drab (as opposed to black) although in the descriptions, *H. wrightii* is said to have a black seed. In both key and descriptions, the surface of mature '*H. micrantha*' seed is described as minutely muricate and the surface of mature *H. wrightii* seed is described as having rounded or truncated pebbling. Large differences in surface sculpture are also indicated in Brackett's illustrations of seed of '*H. micrantha*' and *H. wrightii*. However, no specimens from the West Indies have been seen with seed surface sculpture matching, or even suggesting, that shown in Brackett's Fig. 11. In all specimens examined to date, mature seeds from West Indian plants assigned to *H. wrightii* have had brown, finely muricate seed coats indistinguishable from the seed coats of plants of the Atlantic Coastal Plain. The final reported difference is in the persistence of a greater quantity of dead leaf bases on plants of *H. wrightii*. In this regard, the three plants on the type sheet of *H. wrightii* (*Wright 239*; a specimen not seen by Brackett) are indistinguishable from some specimens collected in the Atlantic Coastal Plain. My own observations suggest that the degree of persistence of dead leaf bases in this species is largely dependent on edaphic factors and is not suitable for taxonomic use.

Hypoxis curtissii Rose in Small, Flora of the Southeastern United States: 287, 1329. 1903. TYPE: Florida: Swamps near Jacksonville, 19 May 1894, *A. H. Curtiss 4727* (HOLOTYPE: US *224588*!; ISOTYPES: F!, MINN!, MO!, NY!)

H. erecta α *leptocarpa* Engelmann & Gray, Boston J. Nat. Hist. 5: 27. 1845. TYPE: Texas, *F. Lindheimer 188* (HOLOTYPE: MO!; ISOTYPES: GH!, PH!)
H. hirsuta var. *leptocarpa* (Engelmann & Gray) Brackett, Rhodora 25: 127. 1923.
H. leptocarpa (Engelmann & Gray) Small, Manual of the Flora of the Southeastern United States:317. 1933.

It is likely that most botanists at the turn of the century assumed *Hypoxis leptocarpa* Engelmann was the valid name for this species since it appeared on widely distributed exsiccatae (*Curtiss 2837* and *Curtiss 4727*), but there is no evidence that the combination was validly published at the specific level prior to Small (1933). Gray, while noting the unpublished use of *leptocarpa* as a specific epithet by Engelmann, explicitly rejected specific status for the taxon (Englemann and Gray, 1845), and cannot be regarded as having published the combination. *Hypoxis curtissii* Rose in Small appears to be the earliest name at the specific level applicable to this species. *H. leptocarpa* (Engelmann & Gray) Small is here treated as a new combination based on *Hypoxis erecta* α *leptocarpa* Englemann & Gray.

Hypoxis rigida Chapman, Flora Southern United States, reprint of ed. 2, Appendix 2: 696. 1892. TYPE: Florida: Apalachicola, *Chapman s.n.* (LECTOTYPE: US *968953*!).

Chapman did not indicate any type specimens in his original description of *Hypoxis rigida,* but potential type specimens from his herbarium were seen at F, MO and US. None of these specimens could be associated unambiguously with the original description of the species. In fact, the original description contains references to characteristics, such as flower number, that suggest that more than a single specimen was used in drawing up the description. A lectotype (US *968953*) is hereby chosen because the specimen, in addition to conforming with the original description as well as other possible types, has mature seed. The specimens examined have very meager collection data, and it is not possible to determine whether any particular specimens were collected together. Accordingly, no isotypes are recognized.

Hypoxis sessilis Linnaeus, Sp. Plantarum, ed. 2: 439. 1762.

No Linnaean specimens of *H. sessilis* are known. The specimen bearing that name in the Linnaean Herbarium (427.19) is a *Cur-*

culigo. Dr. C. F. Barrie (in lit) indicated that this specimen cannot be considered in typification because it evidently entered the herbarium after 1762. Both the fact that the label is in the hand of Linnaeus fil. and the notation Koenig [17]77 (Savage, 1945) indicate the late incorporation of this specimen. Linnaeus cited solely the illustration of *Ornithogali Virginici facie, Herba tuberosa Carolinensis* in Dillenius, Hortus Elthamensis (T. 220, F. 287) when he proposed the species, so, since no specimens corresponding to the Dillenian name have been found in the Dillenian herbarium (Druce and Vines, 1914), that illustration is here designated as the type. Unfortunately, neither the illustration nor the description in Dillenius are diagnostic although they strongly suggest the plant currently called *H. sessilis*. Similarly, the description in Linnaeus is suggestive rather than diagnostic. Like Brackett (1923), I feel that there is nothing to be gained by proposing a new name to replace *H. sessilis*. The Linnaean description and the Dillenian plate refer to a very characteristic feature of the plants currently called *H. sessilis*, namely the shortening of peduncle to a point where the flowers appear to be arising at ground level. This feature seems sufficient to justify the current application of the name even though its use is at variance with most herbarium specimens. Herbarium specimens are typically of plants with peduncles several cm long. In fact, long-peduncled inflorescences are produced relatively infrequently (Herndon, 1988) in natural populations of *H. sessilis*, but these plants are most often collected simply because they are much more visible to collectors than the plants with short peduncles (pers. observ.).

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DEPARTMENT OF BOTANY
LOUISIANA STATE UNIVERSITY
BATON ROUGE, LA 70803

or

FAIRCHILD TROPICAL GARDEN
11935 OLD CUTLER ROAD
MIAMI, FL 33156

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CHROMOSOME NUMBER DETERMINATIONS IN FAM. COMPOSITAE, TRIBE ASTEREAE. IV. ADDITIONAL REPORTS AND COMMENTS ON THE CYTOGEOGRAPHY AND STATUS OF SOME SPECIES OF *ASTER* AND *SOLIDAGO*

JOHN C. SEMPLE, JERRY G. CHMIELEWSKI AND CHUNSHENG XIANG

ABSTRACT

Chromosome numbers are reported for 206 individuals of 100 taxa and three interspecific hybrids from 18 genera. The majority of the reports are for *Aster* and *Solidago,* with about one fourth of these from populations in Alaska, the Yukon, British Columbia, and Alberta. Nearly all counts confirm previous reports for the taxa; some reports are first counts for one or more of the six Canadian provinces or territories and 30 states of the United States sampled. The cytogeography and taxonomy of *Aster puniceus, A. sibiricus* and *A. meritus, Solidago guiradonis, S. confinis, S. spectabilis, S. sparsiflora,* and *S. simplex* are discussed. The following first report is included: *Solidago guiradonis,* $2n = 9_{II}$, $2n = 18$.

Key Words: Compositae, Astereae, chromosome numbers, *Aster, Solidago,* cytogeography, Canada, United States

INTRODUCTION

Determining the distribution patterns of cytotypes requires numerous counts from the range of a taxon. The determinations listed below are reported as contributions to such studies. This is the fourth in a continuing series of general reports on Astereae by the first author's laboratory (Semple, 1985; Semple and Chmielewski, 1987; Semple, Chmielewski and Lane, 1989).

MATERIALS AND METHODS

Meiotic counts were made from pollen mother cells dissected from buds fixed in the field in 3:1/EtOH : glacial acetic acid and subsequently stored under refrigeration in 70% EtOH. Mitotic counts were made from root tip cells taken from transplanted wild rootstocks or from seedlings grown from achenes collected in the wild. Root tips were pretreated in 0.01% colchicine or saturated P.D.B. for 2–3 h, fixed in either Modified Carnoy's Fixative (4:3:1/chloroform : EtOH : glacial acetic acid) or Acetic Alcohol Fixative (3:1/EtOH : glacial acetic acid) and hydrolyzed in 1 N HCl for 30 min at 60° C before squashing. Anther sacs containing

PMCs and meristematic root tips were squashed in 1% acetic orcein, and counts of chromosomes were made from freshly prepared material. Permanent slides were made in most cases as described by Semple, Brammall and Chmielewski (1981) and remain in the possession of J.C.S.

Vouchers for all counts are deposited in WAT. Identifications were made by J.C.S. with the following exceptions. Guy Nesom and Ron Hartman provided identifications for some *Erigeron* collections and confirmed identifications for some *Erigeron, Isocoma,* and *Xylorhiza* collections. In some cases, voucher specimens did not fit a published taxon description in one or more minor traits, such as amount of pubescence; these cases are indicated by the "aff." qualifier in Table 1.

RESULTS AND DISCUSSION

Chromosome number determinations from 206 individuals representing 100 taxa and three interspecific hybrids from 18 genera are reported in Table 1; all location and voucher data are previously unpublished. Populations were sampled in six provinces and territories in Canada and 30 states in the United States. In total, 172 reports are for asters and goldenrods (*Aster, Virgulaster, Virgulus, Solidago* and *Euthamia*). Forty-seven of these are from sites in western Canada and Alaska. Nearly all counts confirm previous reports for the taxa and most are presented without comment. Included in Table 1 is the following first report: *Solidago guiradonis sensu stricto,* $2n = 9_{II}$ and $2n = 18$. Many of the counts are first reports for the taxon or ploidy level of a taxon for a particular state or province; e.g., $2n = 32$ for *Aster puniceus* from Minnesota, $2n = 54$ for *A. schreberi* from Ontario, $2n = 36$ for *Heterotheca camporum* var. *glandulissimum* from Kentucky, $2n = 18$ for *Solidago sempervirens* from Maryland, and $2n = 10$ for *Virgulus campestris* from California.

Aster puniceus

The cytogeography of *Aster puniceus* ($2n = 16$, $2n = 32$) was first discussed and illustrated by Semple et al. (1983). Based on counts from 58 sites reported as of 1983 (Huziwara, 1958; Van Faasen, 1963; Löve and Löve, 1964; Van Faasen and Sterk, 1973; Jones, 1980; Semple and Brouillet, 1980; Semple, 1981; Semple

Table 1. Chromosome number determinations of Astereae from Canada and the United States, arranged alphabetically. *Ah* = T. Ahmed; *Bt* = L. Brouillet; *CC#* = C.C. Chinnappa laboratory collection number; *Ch* = J. Chmielewski; *Hd* = S. Heard; *R* = G. Ringius; *S* = J. Semple; *Su* = Bambang Agus Suripto. When voucher specimens did not fit a published taxon description in one or more minor traits, the "aff." qualifier is used.

Aphanostephus ramosissimus DC. $2n = 8 + 2$ supernumeraries. U.S.A. **Texas.** Howard Co.: Farm Rd. 699 N of Farm Rd. 846, S edge of escarpment, *S 8833.*

Aster alpigenus (Torr. & Gray) Gray ssp. *andersonii* (Gray) Gray. $2n = 36$. U.S.A. **California.** Sierra Co.: Yuba Pass Rd. ca. 1.5 km SE of junction with Nichols Mill Rd., wet meadow, *S, Su & Ah 9325.*

A. anomalus Engelmann in Torr. & Gray. $2n = 16$. U.S.A. **Missouri.** Crawford Co.: E of Steelville, woods by MO-8, *S, Su & Ah 9387.*

A. bracetolatus Nutt. $2n = 16$. U.S.A. **California.** Sierra Co.: S of Loyalton, Antelope Valley Rd., SW of Sierra Brooks, branch of Smithneck Creek, *S, Su & Ah 9317.* **Colorado.** Gunnison Co.: 3.3 km W of Crested Butte, Kebler Pass Rd., *S. & Hd 7756.* **Utah.** Utah Co.: along American Fork Creek, 5 km E of UT-92, *S & Ch 8881*; Weber Co.: UT-39 (MP 34.5) ca. 34 mi. W of Woodruff, *S, Su & Ah 9255.*

A. breweri (Gray) Semple. $2n = 9_{II}$. U.S.A. **California.** Sierra Co.: Yuba Pass Rd. (For.Rd.-12) S of CA-49, SE of Berry Creek, *S, Su & Ah 9319.*

A. chilensis Nees. $2n = 64$. U.S.A. **California.** Contra Costa Co.: Charles Tilden Regional Park, Vollmer Peak, ravine, *S, Su & Ah 9342*; San Mateo Co.: S. San Francisco, by water towers near CA-35, *S & Ch 8913*; Sonoma Co.: W of Glenn Ellen, 6471 Sonoma Mt. Rd., *S, Su & Ah 9329.*

A. ciliolatus Lindl. $2n = 48$. CANADA. **Alberta.** Banff Nat'l. Park: L. Minnewanka Rd. ca. 0.2 mi. from Alta-1, *S & Bt 4349* (count by L. Brouillet). **British Columbia.** Kitwanga, S terminus of the Cassiar Hwy., *Ch et al. CC4761.* **Manitoba.** W of Austin, dirt rd. 0.6 mi. N of TransCanada Hwy. and 2.3 mi. E of MB-352, *S & Bt 4179 & S & Bt 4180* (counts by L. Brouillet).

A. conspicuus Lindl. $2n =$ ca. 108. CANADA. **Alberta.** Jasper Nat'l. Park: Miette Hot Spring Rd. 3.5 S of Alta-16 (in Pocahontas), *S & Bt 4333*; 0.1 mi. from Patricia L., NW of Jasper, *S & Bt 4331.*

A. cordifolius L. $2n = 16$. U.S.A. **Vermont.** Caledonia Co.: W of town of Wells River, US-302 1.5 mi W of US-5, *S & Bt 3518* (count by L. Brouillet). $2n = 16 + 2–3$ supernumeraries. **Pennsylvannia.** York Co.: PA-372 woods below bridge over Susquehana R., *S & R 7611.* $2n = 32$. CANADA. **Ontario.** Waterloo R.M.: Wellesley Twp., *S & Ch 9098.* $2n = 48$. U.S.A. **North Carolina.** Macon Co.: NC-28 N of Gneiss, *S & Ch 6219.*

A. aff. *cordifolius* L. $2n = 32$. CANADA. **Ontario.** Waterloo R.M.: Wellesley Twp., *S & Ch 9100.*

A. cordifolius × *A. pilosus* var. *pilosus.* $2n = 32$. CANADA. **Ontario.** Waterloo Co.: Wellesley Twp., along farm rd., *S & Ch 9099.*

A. dumosus L. $2n = 32$. U.S.A. **South Carolina.** Florence Co.: US-51 N of Pamplico, *S & Ch 6116.*

A. elliotti Torr. & Gray. $2n = 16$. U.S.A. **Florida.** Lake Co.: FL-46 at Wekiwa R., *S et al. 5342.*

Table 1. Continued.

A. foliaceus Lindl. $2n = 64$. U.S.A. **Utah.** San Pete Co.: E of Ephraim, rd. to top of Wasatch Plateau, *S & Ch 8891*. Summit Co.: Wasatch N.F., For. Rd. just E of UT-150 just S of N.F. border, *S, Su & Ah 9213*. **Wyoming.** Carbon Co.: S of Arlington, Rocky Creek Trail, ca. 2 km S of I-80, *S, Su & Ah 9205*.

A. laevis L. var. *laevis*. $2n = 48$. CANADA. **British Columbia.** N of Windermere, Lake Drive by Wenderemere L., disturbed woods, *S & Bt 4361* (count by L. Brouillet). U.S.A. **Montana.** Silver Bow Co.: SE of Butte, near Continental Drive, ca. 2 mi. E of access to I-90, *S & Bt 4422* (count by L. Brouillet).

A. lanceolatus Willd. ssp. *hesperius* (Gray) Semple & Chmielewski. $2n = 64$. U.S.A. **Arizona.** Yavapai Co.: US-89 (MP309) SE of Prescott, by creek, *S & Ch 8998*.

A. lanceolatus ssp. *lanceolatus* var. *hirsuticaulis* Semple & Chmielewski. $2n = 32$. U.S.A. **Wisconsin.** Bayfield Co.: WI-27 21.3 km S of Douglas Co. Rd. A, S of Barnes, *S 9084*. Douglas Co.: Co. Rd.-U S of Amnicon Falls State Park, *S 9070*.

A. lanceolatus ssp. *lanceolatus* var. *lanceolatus*. $2n = 64$. U.S.A. **Wisconsin.** Douglas Co.: Co. Rd.-U S of Amnicon Falls State Park, *S 9071*.

A. lanceolatus ssp. *lanceolatus* × *A. pilosus* var. *pilosus*. $2n = 48$. CANADA. **Ontario.** Waterloo Co.: Wellesley Twp., by RR, *S & Ch 9096*.

A. lateriflorus (L.) Britt. $2n = 16$. U.S.A. **North Carolina.** Wilson Co.: NE of Eureka, NC-222 2 mi. N of county line, *S & Ch 6009*. $2n = 32$. **Pennsylvania.** Centre Co.: Nittany Mts., PA-144 just W of Pleasant Gap, *S & R 7602*.

A. aff. *lentus* Greene. $2n = 64$. U.S.A. **California.** Napa Co.: Vallejo, junction of Fairground Rd. and American Cr., SE of Napa, *S & Ch 8912*.

A. longifolius Lam. $2n = 80$. U.S.A. **Wisconsin.** Douglas Co.: WNW of Barnes, pond near WI-27, *S 9078*.

A. linariifolius L. $2n = 18$. U.S.A. **Florida.** Okaloosa Co.: US-90, E of Crestview, 2 mi W of Shoal R., *S. Bt & Canne 3893*. **Mississippi.** Simpson Co.: MS-13 0.6 mi N of MS-28, S of Mendalhall, *S, Bt, & Canne 3815*.

A. macrophyllus L. $2n = 72$. CANADA. **Nova Scotia.** Yarmouth Co.: NS-340 just N of Carleton, *S & Keir 4858*. U.S.A. **Pennsylvania.** Elk Co.: US-219 S of Ridgeway, N of Hwy.-948, *S & R 7594*. **Wisconsin.** Sheboygan Co.: Kettle Moraine State For., Kettle Hole Geological Marker Site, slopes of kettle hole. *S 9091*.

A. modestus Lindl. $2n = 18$. CANADA. **Alberta.** Jasper Nat'l. Park: N of Alta-16, W of Clairvaux Creek (trail site), *S & Bt 4323*. **British Columbia.** Cassiar Hwy. 33 km S of Cassiar, Mighty Moes Campground, KP580.2, edge of Cotton L., *Ch et al. CC4726*.

A. occidentalis Nutt. $2n = 16$. U.S.A. **California.** Plumas Co.: CA-89 SW of Crescent Mills, *S et al. 5719*.

A. oolentangiensis Riddell. $2n = 32$. U.S.A. **Wisconsin.** Douglas Co.: WNW of Barnes, margins of kettle hole pond by WI-27, 2.1 km N of Co. Rd.-A, *S 9082*.

A. aff. *parviceps* (Burgess) Mackenzie & Bush. $2n = 32$. U.S.A. **Missouri.** Washington Co.; MO-8 6.6 km W of Potosi, *S, Su & Ah 9393*.

A. pilosus Willd. var. *pilosus*. $2n = 32$ U.S.A. **Arkansas.** Dallas Co.: N of Princeton, AR-9 just N of AR-48, *S & Ch 6402*. **Tennessee.** Williamson Co.: TN-96 E

Table 1. Continued.

of Triune, *S & Ch 6289*. **West Virginia.** Hampshire Co.: WV-28 4.5 mi. S of Springfield, *S & Ch 5883*. $2n = 48$. U.S.A. **Kentucky.** Hopkins Co.: KY-109 1 km N of Charleston, *S & Su 9431*.

A. pilosus Willd. var. *pringlei* (Gray) Blake. $2n = 48$. U.S.A. **Massachusetts.** Berkshire Co.: S of Otis, MA-8 0.9 mi. S of MA-23, *S & Bt 3628*. **Virginia.** Northumberland Co.: Reedville, *S & Ch 5988*.

A. prenanthoides Muhl. $2n = 32$. U.S.A. **New York.** Hamilton Co.: NY-28 by Eighth L., *S & Bt 3665*. Lewis Co.: Lowville, NY-26 0.1 mi S of NY-12 & 26, *S & Bt 3650*.

A. priceae Britt. $2n = 64$. U.S.A. **Tennessee.** Trousdale Co., US-231 3.3 km N of Cumberland R., *S & Ch 9129*.

A. puniceus L. $2n = 16$. CANADA. **Ontario.** Prescott Co.: Hwy-17 between Alfred and Plantagenet, picnic area, *S 2413*. U.S.A. **Michigan.** Mackinac Co.: US-2 10.6 mi. E of Naubinway, *S & Ch 5007*. $2n = 32$. **Minnesota.** Mille Lacs Co.: US-169 between Rum River Rest Area and rd. to Onamia, *S 9064*.

A. radulinus Gray. $2n = 27$ (triploid). U.S.A. **California.** Mendocino Co.: E of Ft. Bragg, CA-20 at Chamberlain Creek For. Demonstration Area picnic ground, *S & Hd 8552*. (This is the same population sampled as *S et al. 5677* and previously reported as triploid by Semple et al., 1983)

A. reticulatus Pursh. $2n = 18$. U.S.A. **Florida.** Liberty Co.: NW of Sumatra, near branch of Kennedy Creek by Fl-379, *Godfrey s.n.* (fruit collection only).

A. schreberi Nees. $2n = 54$. CANADA. **Ontario.** Halton Reg. Mun.: S of Waterdon, Grindstone Creek Valley, *S, Bradley & Axon 9047*. York Co.: Richmond Hill, golf course, *Ch & Cameron 2337*.

A. shortii Lindl. in Hook. $2n = 16$. U.S.A. **Tennessee.** Marshall Co.: Henry Horton State Park, Wilhoite Mill Hiking Trail, *S & Ch 9116*.

A. sibiricus L. $2n = 18$. CANADA. **Alberta.** Ghost River Valley, *Chinnappa & Ch CC4906*. Jasper Nat'l. Park: Sunwapta Pass, *S & Bt 4347*. **British Columbia.** Cassiar Hwy., 53 km N of Good Hope, 52 km S of Alaska Hwy., *Ch et al. CC4713*; Chilkat Pass, base of Nadahini Mt., Haines Hwy., KmP147.7, *Ch et al. CC3959*; Teska River Flats, Alaska Hwy., KmP600, *Ch et al. CC3775*. **Yukon.** Carcress Desert N of Carcress, Klondike Loop 2, S of Whitehorse, *Ch et al. CC3882*; Dempster Hwy., KmP107-108, beside Blackstone River, *Ch et al. CC4512*; NE of Stewart Crossing, Siver Trail Hwy., KmP19, *Ch et al. CC4564*; 5 km S of Pelly Crossing, Klondike Loop, KmP460,*Ch et al. CC4601*; South Canol Rd., KmP165, Lapie L. access rd., *Ch et al. CC4676, Ch et al. CC4677*; junction of Sheep Creek and Rose River, *Ch et al. CC4691*. U.S.A. **Alaska.** 7 km S of Deadhorse, Dalton Hwy., MP407, Prudhoe Bay, *Ch et al. CC4387*; Edgerton Hwy., MP26-25, 7 mi. N of Chitina, *Ch et al. CC4069*; Edgerton Hwy. near Kennicott River, *Ch et al. CC4080*; just NW of Kiskulana Bridge, MP14, *Ch et al. CC4075*; Richardson Hwy., 7.7 km N of McCullen Creek, 35 km N of Paxson, *Ch et al. CC4087*; Glenn Hwy., 6 km E of Little Nelchina R. Bridge, near Nelchina State Hwy. maintenance station, *Ch et al. CC4111*; Pond E of KmP137.3, Long L., *Ch et al. CC4134*; NE of Fairbanks, Chena Hot Springs Rd., MP39.5, Granite Tours Trailhead, N Fork of Chena River, *Ch et al. CC4233*; Elliot Hwy., just SW of Baker

Table 1. Continued.

Creek, MP138, *Ch et al. CC4281*; Dalton Hwy., 12.2 mi. N of Coldfoot, MP187.2, *Ch et al. CC4291*.

A. simmondsii Small. $2n$ = ca. 64. U.S.A. **Florida.** Indian River Co.: E of Fellsmere, Co. Rd.-512 just E of I-95, *S 7525*.

A. tradescanti L. $2n$ = 16. CANADA. **Nova Scotia.** Yarmouth Co.: NW of Carleton, NS-340 S of Richfield, edge of lake, *S & Keir 4860*. U.S.A. **Vermont.** Windham Co.: Rockingham, *S 6884*.

A. umbellatus Mill. var. *pubens* Gray. $2n$ = 18. U.S.A. **Wisconsin.** Douglas Co.: US-2 E of Maple, *S 9703*.

A. undulatus L. $2n$ = 32. U.S.A. **Alabama.** Cleburne Co.: N of Chulafinnee, US-431 5 mi. S of I-20, *S & Ch 6310*.

A. urophyllus Lindl. $2n$ = 16. U.S.A. **New York.** Cattaraugus Co.: 7.6 km N of Ellicottville, *S & R 7570*. **Minnesota.** Crow Wing Co.: Nisswa, *S & Hd 8790*. **Missouri.** Washington Co.: MO-8 6.6 km W of Potosi, *S, Su & Ah 9391*. **Wisconsin.** Bayfield Co.: WI-27 21.3 km S of Co. Rd.-A, S of Barnes, *S 9085*.

Chrysopsis godfreyi Semple f. *viridis* Semple. $2n$ = 10. U.S.A. **Florida.** Bay Co.: Tyndall A.F.B., NCO Beach East, progeny of *A. Johnson 8016a*.

C. mariana (L.) Ell. $2n$ = 8. U.S.A. **Florida.** Liberty Co.: FL-20 opposite Hosford Fire Tower, *S & Godfrey 3101*.

Erigeron aff. *aequilifolius* Hall. $2n$ = 18. U.S.A. **California.** Tulare Co.: For. Rd. J-41 E of Johnsondale, 11.5 km W of Sherman Pass Summit, *S & Hd 8652*.

E. acris L. ssp. *politus* (E. Fries) Schinz & Keller. $2n$ = 18. CANADA. **Alberta.** Jasper Nat'l. Park: ca. 3 mi. W of Jasper, *S & Bt 4328*.

E. divergens Torr. & Gray. $2n$ = 18. U.S.A. **California.** Mono Co.: N of Lee Vining, shore of Mono L., *S & Hd 8719*. $2n$ = 36. **New Mexico.** Taos Co.: NW of Holman, NM-3, MP53, Sipapu Ski Area, *S & Hd 8069*.

E. eatonii Gray. $2n = 9_{II}$. U.S.A. **Wyoming.** Albany Co.: Medicine Bow Nat'l. For., S of Lincoln Monument (I-80 at Happy Jack Rd.), *S 8797*.

E. foliosus Nutt. var. *hartwegii* (Greene) Jeps. $2n$ = 18. U.S.A. **California.** Del Norte Co.: US-199 W of Gasquet, *S & Hd 8520*.

E. formosissimus Greene var. *formosissimus*. $2n$ = 18. U.S.A. **Arizona.** Coconino Co.: N of Flagstaff, SnoBowl Rd., below ski area, *S & Ch 9002*.

E. formosissimus Greene var. *viscidus* (Rydb.) Cronq. $2n$ = 18. U.S.A. **New Mexico.** Taos Co.: N of Vadito, NM-3 3.5 km N of NM-75, *S & Hd 8065*.

E. inornatus (Gray) Gray. $2n$ = 18. U.S.A. **California.** Siskiyou Co.: SW of Etna, S of Etna Summit, *S & Hd 8485*.

E. simplex Greene. $2n$ = 18. U.S.A. **Colorado.** Chaffee Co.: W of Poncha Springs, US-50 4.4 km E of Monarch Pass, *S & Hd 7741*.

E. speciosus (Lindl.) DC. $2n$ = 18. U.S.A. **Arizona.** Coconino Co.: N of Flagstaff, Schultz Pass Rd., N of US-180, *S & Ch 9006*.

E. subtrinervis Rydb. $2n$ = 18. U.S.A. **New Mexico.** Lincoln Co.: W of Alto, NM-532, Sierra Blanca Ski Area, *S & Hd 8094*.

Euthamia graminifolia (Salisb.) Nutt. $2n$ = 18. U.S.A. **Delaware.** Sussex Co.: US-9, E of Georgetown, 3 km W of DL-30, *S & R 7643*. **Wisconsin.** Douglas Co.: WNW of Barnes, pond near WI-27, 2.1 km N of Co. Rd.-A, *S 9077*.

Grindelia camporum Greene. $2n$ = 12. U.S.A. **California.** Glenn Co.: NW of Alder

Table 1. Continued.

Springs, For. Hwy.-7, *S & Hd 8564*. Stanislaus Co.: W of Patterson, Co. Rd. J-17 2.3 km E of Minnear Campground, Frank Raines Park, *S & Hd 8584*.

Haplopappus gracilis Nutt. $2n = 4$. U.S.A. **New Mexico.** Catron Co.: US-180 W of Luna, 5.5 mi. E of state line, *S & Hd 8029*.

H. squarrosus Hook. & Arn. $2n = 10$. U.S.A. **California.** Monterey Co.: Rd. G-14 S of King City, just N of Liggett Military Base, *S & Ch 8939*; S of Big Sur, E of Pfeiffer Beach, *S & Ch 8930*. Ventura Co.: N of Ventura, Santa Ana Rd. W of CA-33, *S. & Ch 8968*.

Heterotheca camporum (Greene) Shinners var. *glandulissimum* Semple. $2n = 36$. U.S.A. **Kentucky.** Warren Co.: US-213 10.9 km SE of I-65, S of Bowling Green, *S & Ch 9103*.

H. psammophila Wagenknecht. $2n = 18$. U.S.A. **Arizona.** La Paz Co.: US-60 just W of Wendon, *S & Ch 8994*.

Isocoma veneta (H.B.K.) Greene. $2n = 24$. U.S.A. **California.** Santa Barbara Co.: CA-1 ca. 1 mi. S of CA-135, MP30.1, *S & Ch 8964*. San Diego Co.: Del Mar, near beach, *S & Ch 8992*.

Leucelene ericoides (Torr.) Greene. $2n = 32$. U.S.A. **Arizona.** Coconino Co.: SW of Winslow, AZ-87 6.6 km SW of county line, *S & Hd 7913*.

Machaeranthera tanacetifolia H.B.K. $2n = 4_{II}$. U.S.A. **Arizona.** Apache Co.: McCarrell Rd by I-40, ca 3 mi. W of Chamber, *S, Su & Ah 9367*.

Pityopsis falcata (Pursh) Nutt. $2n = 18$. U.S.A. **Massachusetts.** Barnstable Co.: junction of MA-137 and Long Pond Rd., *S 3366*.

Prionopsis ciliata (Nutt.) Nutt. $2n = 12$. U.S.A. **Texas.** Howard Co.: S of Big Spring, FR-700, *S & Hd 8210*.

Pyrrocoma apargioides (Gray) Greene. $2n = 12$. U.S.A. **California.** Mono Co.: CA-108 a few km W of US-395, picnic area W of Walker R., *S & Hd 8722*.

P. uniflora (Hook.) Greene. $2n = 24$. U.S.A. **Utah.** Emery Co.: UT-29 15.1 km W of UT-57, W of Orangeville, *S & Hd 7802*.

Solidago altissima L. var. *altissima*. $2n = 54$. U.S.A. **Nebraska.** Jefferson Co.: US-136 3 mi. N of county line, *S & Bt 7349*.

S. altissima L. var. *gilvocanescens* (Rydb.) Semple. $2n = 36$. U.S.A. **Minnesota.** Olmsted Co.: US-14 (MP206), SW of Rochester, *S 9056*.

S. arguta Ait. $2n = 18$. U.S.A. **North Carolina.** Transylvania Co.: US-276 near Connestee Falls, *S & Ch 6174*.

S. caesia L. $2n = 18$. U.S.A. **Delaware.** New Castle Co.: DL-82 S of Yorklin, ca. 4 km W of DL-52, *S & R 7620*. **Kentucky.** Adair Co.: NW of Toria, beech woods near Cumberland Parkway (MP38.1), *S & Su 9445*. Christian Co.: KY-109 SE of Dawson Spring, N end of Pennyrile Forest St. Pk, *S & Su 9432*. **Maryland.** Washington Co.: US-40 N of Greenbrier State Park, *S & R 7658-1*. **Pennsylvania.** York Co.: PA-372, below W side of bridge at Susquehana R., *S & R 7608*.

S. californica Nutt. $2n = 9_{II}$. U.S.A. **California.** San Benito Co.: W of Hernandez, Coalinga Rd., Lorenzo Vasques Cyn., *S, Su & Ah 9346*.

S. canadensis L. aff. var. *canadensis*. $2n = 36$. U.S.A. **Tennessee.** Davidson Co.: junction of TN-171 and US-41, *S & Ch 9124*.

S. canadensis L. ssp. *salebrosa* (Piper) Keck. $2n = 18$. U.S.A. **Wyoming.** Teton

Table 1. Continued.

Co.: US-26 0.3 mi. E of Teton N.F. boundary, *S & Bt 7219*. $2n = 36$. **Colorado.** Gunnison Co.: N of Gunnison, CO-135 7.3 km S of Almont, *S & Hd 7752*. $2n = 54$. **Montana.** Musselshell Co.: US-12 4.2 mi. W of Musselshell, *S & Bt 6993*.

S. confinis Gray. $2n = 18$. U.S.A. **California.** Kern Co.: E of Bakersfield, Kern R. canyon, Democrat Flat springs, *S, Su & Ah 9362*. Ventura Co.: N end of Fillmore, *S & Ch 8970*.

S. guiradonis Gray. $2n = 9_{II}$. U.S.A. **California.** San Benito Co.: SW of New Idria along Clear Creek, Clear Creek Rd. 4.65 km NE of Coalinga Rd., *S, Su & Ah 9349*, 7.15 km NE of Coalinga Rd., *S, Su, & Ah 9352*. $2n = 18$. **California.** San Benito Co.: SW of New Idria, Clear Creek Rd. 7.3 km NE of Coalinga Rd., along Clear Creek, *S, Su & Ah 9354, S, Su & Ah 9355*.

S. hispida Muhl. var. *tonsa* Fern. $2n = 18$. CANADA. **Ontario.** Lambton Co.: Pinery Prov. Park, *Bakowsky s.n.*

S. juncea Ait. $2n = 18$. U.S.A. **Minnesota.** Sherburne Co.: US-169 near Mississippi R., S of Elk River, *S 9060*.

S. multiradiata Ait. $2n = 18$. CANADA. **British Columbia.** S of Chilkat Pass, Haines Hwy., Jarvis Glacier area, Mt. McDonnell, S of Seltat Creek, *Ch et al. CC3920*.

S. nana Gray. $2n = 18$. U.S.A. **Colorado.** Gunnison Co.: Kebler Pass Rd. 14.8 km E of CO-133, E of Somerset, *S & Hd 7779*. (This is a correction of a previous report for *S. sparsiflora* in Semple and Chmielewski 1987; see text for discussion.)

S. parryi (Gray) Greene. $2n = 18$. U.S.A. **Utah.** Sevier Co.: ca. 18 km S of Gooseberry, near Gooseberry Rd., *S & Ch 8895*.

S. petiolaris Ait. var. *petiolaris*. $2n = 36$. U.S.A. **North Carolina.** Richmond Co.: US-1, 4.6 mi. S of NC-220, *S, Brammall & Hart 3044*.

S. ptarmicoides (Nees) Boivin. $2n = 18$. U.S.A. **Wisconsin.** Douglas Co.: WNW of Barnes, near pond near WI-27, 2.1 km N of Co. Rd.-A, *S 9075*.

S. rigida L. ssp. *humilis* (Porter) Heard & Semple. $2n = 18$. U.S.A. **Minnesota.** Sherburne Co.: US-169 near Mississippi R., S of Elk River, *S 9057*.

S. rigida L. ssp. *rigida*. $2n = 36$. U.S.A. **Illinois.** Livingston Co.: E of Forrest, between US-24 and RR, *S & Bt 7386*. Stephenson Co.: US-20 E of Freeport, *S 9050*. **Indiana.** Benton Co.: US-52 just NW of Fowler, *S & Hd 8335*. **Minnesota.** Sherburne Co.: Olmstead Co.: US-14 (MP206), SW of Rochester, *S 9054*.

S. rugosa Mill. $2n = 18$. CANADA. **Ontario.** Wellington Co.: Arkell, *S 7397*. $2n = 36$. U.S.A. **Delaware.** Sussex Co.: US-9 3 km W of DL-30, E of Georgetown, *S & R 7641*. **Maryland.** Washington Co.: US-40 N of Greenbrier State Park, *S & R 7655*. $2n = 54$. **New York.** Chattaraugus Co.: N of Ellicottville, *S & R 7571*.

S. sempervirens L. $2n = 18$. U.S.A. **Delaware.** Sussex Co.: near DL-1, by Delaware Sea Shore State Park, *S & R 7648*. **Maryland.** US-301 1 km E of Drawbridge, N of Grasonville, *S & R 7633*.

S. simplex Kunth ssp. *simplex* var. *simplex*. (syn: *S. glutinosa* var. *glutinosa*). $2n = 18$. CANADA. **British Columbia.** Alaska Hwy., KP600, Teska River flats,

Table 1. Continued.

just N of Teska service station, *Ch et al. CC3773*; Alaska Hwy., 21 km SE of Fireside, *Ch et al., CC3783*; Cassiar Hwy., 6 km N of Boya L. Provincial Park turnoff, *Ch et al., CC4720*; Cassiar Hwy., KP729.8, at Yukon border, *Ch et al., CC4709*; 12 km N of Iskutm just N of Tsasbye Creek, *Ch et al., CC4752*; Telegraph Creek Rd., 1 km NE of Telegraph Creek, *Ch et al., CC4738*; Telegraph Creek Rd., 40 km S of Dease L., , *Ch et al., CC4735*; Telegraph Creek Rd., 5 km S of Dease L., *Ch et al., CC4731*. **Yukon.** Campbell Hwy., KP570, 21 km SE of Carmacks Junction, *Ch et al., CC4606*; Campbell Hwy., KP560, just N of turnoff to Frenchman L. Gov't. Campground, *Ch et al., CC4608*; Campbell Hwy., KP539, N of turnoff to Frenchman L. Gov't. Campground, *Ch et al., CC4610*; Campbell Hwy., KP410, 10 km SE of Faro Junction, *Ch et al., CC4614*; S of Whitehorse, Klondike Loop 2, KP108.3, *Ch et al., CC3883*; Klondike Loop 2, 2 km N of MacGregor Creek, KP406-407, *Ch et al., CC4604*; 5 km S of Pelly Crossing, Klondike Loop, KP460, *Ch et al., CC4600*. U.S.A. **Alaska.** N of Dot L., Alaska Hwy., KP1367.5, *Ch et al., CC4470*; Dempster Hwy., KP12.2, *Ch et al., CC4561*; Glenn Hwy., 1 km E of Tolsona Lake Rd., W of Tolsona Creek, *Ch et al., CC4102*; Siver Trail Hwy., NE of Stewart Crossing, KP19, *Ch et al., CC4563*.

S. sparsiflora Gray. $2n = 18$. U.S.A. **Texas.** Culberson Co.: Guadalupe Mountain Nat'l. Park, Bowl Trail, 7700′, *S & Hd 8180*. $2n = 36$. **Arizona.** Coconino Co.: N of Flagstaff, SnoBowl Rd., below ski area, *S & Ch 9003*.

S. spectabilis (D.C. Eaton) Gray. $2n = 18$. U.S.A. **California.** Modoc Co.: CA-299 12.5 km W of Alturas, N of Rattlesnake Butte, *S, Su & Ah 9299*. Shasta Co.: CA-299, Hat Creek Park, Shasta N.F., near Pit R., bank of Hat Creek, *S, Su & Ah 9301*.

S. uliginosa Nutt. $2n = 18$. U.S.A. **Minnesota.** Aitkin Co.: SW of McGrath, bog by MN-18 4 km E of MN-65, *S 9067*. **Wisconsin.** Portage Co.: NE of Stevens Point, WI-10 E of WI-34, marsh, *S 9086*.

S. wrightii Gray. $2n = 9_{II}$. U.S.A. **Arizona.** Pima Co.: Mt. Lemmon, near summit, *S, Hd & Love 7929*. $2n = 18$. **Arizona.** Yavapai Co.: just E of Prescott, US-89 (MP317), *S & Ch 9000*. **New Mexico.** Grant Co.: NM-15 39.2 km N of US-180, N of Silver City, *S & Ch 9039*.

Virgulaster ascendens (Lindl.) Semple. $2n = 13_{II}$. U.S.A. **Arizona.** Coconino Co.: Spring Valley, 6 mi N of Parks, *S et al. 5563*. $2n = 26$. **California.** Sierra Co.: CA-49 W of Yuba Pass, campground, *S & Hd 8407*. $2n = 52$. **Utah.** Salt Lake Co.: E of Midvale, UT-190, lower end of Big Cottonwood Cyn, *S, Su & Ah 9239*.

Virgulus × *amethystinus* (Nutt.) Reveal & Keener (*V. ericoides* × *V. novae-angliae*). $2n = 10$. CANADA. **Ontario.** Waterloo Co.: Wellesley Twp., by RR, *S & Ch 9093*.

V. campestris (Nutt.) Reveal & Keener. $2n = 10$. CANADA. **British Columbia.** BC-95 2 km N of Edgemont, 12 km N of Radium, *Ch CC4899*. U.S.A. **California.** Mono Co.: town of Mammoth Lakes, *S & Hd 8685*.

V. concolor (L.) Reveal & Keener. $2n = 8$. U.S.A. **Florida.** Leon Co.: W of Tallahassee, *Godfrey 82228*.

V. ericoides (L.) Reveal & Keener var. *ericoides*. $2n = 10$. CANADA. **Ontario.**

Table 1. Continued.

Waterloo Reg. Mun.: Wellesley Twp, *S & Ch 9094*. $2n = 20$. U.S.A. **Illinois.** Winnebago Co.: Kilbuck Bluffs Forest Reserve, SW of Rockford, *S 9048*.

V. ericoides var. *pansus* (Blake) Reveal & Keener. $2n = 10$. U.S.A. **Arizona.** Yavapai Co.: US-89 NE of Peoples Valley, *S & Ch 8995*. **Utah.** Uintah Co.: US-191 2.2 km N of Vernal, *S & Ch 8874*.

V. falcatus (Lindl.) Reveal & Keener. $2n = 30$. U.S.A. **Colorado.** Boulder Co.: E of Lyons, *S et al. 5815*.

V. patens (Ait.) Reveal & Keener var. *patens*. $2n = 20$. U.S.A. **Georgia.** Gordon Co.; S bound rest area, I-75 N of Calhoun, *S et al. 7403*.

V. patens var. *patentissimus* (Torr. & Gray) Reveal & Keener. $2n = 20$. U.S.A. **Arkansas.** Yell Co.: E of Danville, AR-10 13.9 km W of AR-7, *S & Hd 8288*.

Xylorhiza tortifolia (Torr. & Gray) Greene. $2n = 12$. U.S.A. **Utah.** Garfield Co.: UT-95 at View Point Rd., W of L. Powell and Hite Marina, *S 8818*.

et al., 1983), Semple et al. (1983) noted that diploids occurred throughout the species' range. The few known tetraploids came from its western margin near the prairies in central Canada and the midwestern United States.

Authenticity of the one tetraploid report from northeastern Iowa (Semple et al., 1983) has come into question, and thus it should be accepted only with caution. We have discovered that the plant in the greenhouse at Waterloo confirmed to be tetraploid *A. puniceus* had the same collection number as a second plant, a tetraploid *A. ontarionis*; thus the Iowa provenance of the *A. puniceus* plant is not certain.

Since 1983, 75 additional sites have been sampled by this laboratory or others, and the distribution of diploids and tetraploids conforms to the pattern illustrated by Semple et al. (1983). Diploids were found at 74 sites in Nova Scotia and Ontario in Canada, and Maine, Michigan, Minnesota, and Virginia in the United States (Table 1; Hill, 1983; Semple, 1985; Chmielewski, 1987). An additional tetraploid (with the *lucidulus* morphotype) was found in eastern Minnesota (Table 1) near the edge of the range. Thus, although one of the four previous tetraploid reports is questioned, the new report replaces it to maintain the pattern as first presented.

Aster sibiricus and A. meritus

In North America, *Aster sibiricus* L. was found to be diploid $2n = 18$ at 43 sites in Alaska, Alberta, British Columbia, North-

west Territories, and the Yukon (Table 1; Mulligan et al., 1972; Semple and Brouillet, 1980; Chinnappa and Chmielewski, 1987). *Aster meritus* A. Nels. has been reported to be tetraploid at four sites in Montana and northwestern Wyoming (Semple et al., 1983; Semple, 1985). The habitats and ranges of the two species do not appear to overlap. *Aster sibiricus* is an alpine/tundra taxon of northern Eurasia, Alaska, and western Canada. *Aster meritus* is a montane to subalpine taxon of the northcentral Rocky Mountains in the United States; it has been treated as *A. richardsonii* Spreng. var. *meritus* (A. Nels.) Raup and *A. sibiricus* L. var. *meritus* (A. Nels.) Raup. Although the two taxa are closely related, we feel species status is more appropriate for the more southern member of the complex. Additional study, however, is recommended to clarify the status of *A. meritus* and its relationship to *A. radulinus*.

Solidago guiradonis, S. confinis and S. spectabilis

Solidago guiradonis, S. confinis, and *S. spectabilis* clearly form a closely related species complex that is the far western element of the *S. missouriensis/S. juncea* group of goldenrods. Guirado's goldenrod in the strict sense is an endemic restricted to ultramafic arroyo and creek margins in southern San Benito County, California and adjacent Fresno County. It is morphologically close to and perhaps conspecific with *Solidago confinis,* which occurs in usually boggy or marshy ground and creek margins from San Benito County southward in the coastal ranges and northern Inyo County southward in the Sierras to northern Baja California. Solbrig et al. (1964), Beaudry (1969) and Semple et al. (1989) reported *S. confinis* to be diploid in southern California. The two species differ primarily in basal leaf width and in branching pattern in the club-shaped capitulescence; *S. guiradonis* is narrower in both traits. The counts of $2n = 9_{II}$ and $2n = 18$ (Table 1) are the first reports for *S. guiradonis* in the strictest sense. However, a report by Raven et al. (1960) for *S. confinis* from San Benito County (*Solbrig 2816* DS!, CAS!) may represent the first report for *S. guiradonis,* if a broader interpretation of the latter species is adopted. Based on field observations of a number of small and large populations of both taxa, there appears to be only a limited morphological basis on which to separate the two. Character states for diagnostic traits of *Solidago guiradonis* appear only to be extremes at the lower limits of much greater ranges of variation

included in *S. confinis*. It would not be unreasonable to merge the two species under the older name *S. guiradonis* and treat the two at some infraspecific rank. The significance of environmental factors on morphology needs further study; *S. guiradonis s.s.* is endemic to special ultramafic soils and *S. confinis* is not. For clarity we have presented our reports under two names.

Individuals of *Solidago confinis* can be difficult to separate from *S. spectabilis* (D.C. Eaton) Gray, which is native to moist habitats in the Great Basin area and adjacent Sierra Nevadas. The ranges of the two overlap in Inyo and Kern Counties in California. Broad phyllary tips with flat margins are generally diagnostic features of *S. spectabilis*; both *S. confinis* and *S. guiradonis* have narrow phyllary apices with inrolled margins. The number of ray florets does not appear to be diagnostic for any of these three taxa. A multivariate analysis of morphological variation should be undertaken to determine which traits best distinguish the three taxa.

Solidago sparsiflora

Solidago sparsiflora is one of several closely related goldenrod taxa native to the southwestern United States and Mexico; the other two are *S. californica* Nutt. and *S. velutina* DC. Taylor and Taylor (1984) treated *S. sparsiflora* as a subspecies of *S. velutina* with the combination *S. velutina* ssp. *nevadensis* (A. Gray) Taylor and Taylor. Nesom (1989b) noted that the complex included additional Mexican species, and Semple et al. (1990) noted the need for additional study of the complex, which is similar to *S. nemoralis* of the prairies and woodlands of eastern North America. Each member of the complex has a distinct geographic range, and thus the cytogeography of each can be examined separately with caution. Regardless of the epithet applied, a sufficient portion of the range has been sampled to permit some generalizations regarding the cytogeography of *S. sparsiflora*. In total, counts have been reported for 38 locations from the United States (Table 1; Raven et al., 1960; Anderson et al., 1974; Ward and Spellenberg, 1986, as *S. velutina* ssp. *nevadensis*; Semple et al., 1984; Semple, 1985; Semple and Chmielewski, 1987; Semple et al., 1989). Diploids ($2n = 18$) are known from Arizona (12 sites throughout the state), Colorado (six sites generally in the central part of the state), Nevada (one site west of Las Vegas), Texas (Guadalupe Mt.), and Utah (four sites). Tetraploids ($2n = 36$) have been less frequently collected: Arizona (one site near Flagstaff), New Mexico (four

sites), Nevada (one site near Utah), Utah (two sites in the Wasatch Plateau), and Wyoming (one site in the Big Horn Mts.). The single report for a hexaploid ($2n = 54$) is from a site west of Boulder, Colorado. Polyploids occur throughout the range in the United States, but represent a greater portion of the sample in the northern part of the range (five out of the 15 sites north of the 37th parallel) than in the southern part of the range of the species (four out of 24 sites south of the 37th parallel). In addition, the species has been reported to be diploid at three locations in central Mexico (Ward and Spellenberg, 1986). Any study meant to clarify the most suitable rank to assign *S. sparsiflora* will have to take into consideration the fact that the taxon occurs at three ploidy levels. Brammall and Semple (1990) and Semple et al. (1990) determined that in the related *S. nemoralis* complex ploidy level was significant in distinguishing subspecies but was not diagnostic.

In the course of examining vouchers for this report, the voucher for one diploid report for *S. sparsiflora* (Semple and Chmielewski, 1987) was determined to be *S. nana* (location given in Table 1). *Semple and Heard 7799* (WAT!) has the more corymbiform capitulescence and the short dense pubescence on its stems and leaves generally characteristic of *S. nana*. The voucher was collected well after blooming; the involucres at flowering would probably have been larger than normal for *S. sparsiflora*. The voucher is part of the same taxon as the voucher for the only other report for *S. nana* (Semple et al., 1989), which was also diploid.

Solidago simplex

Ringius and Semple (1987) discussed the cytogeography of this species throughout its range under the synonym *Solidago glutinosa*. Nesom (1989a) noted that the types of *S. simplex* and *S. glutinosa* were conspecific and that the former name was older and had nomenclatural priority. Ringius and Semple (1987) determined that all reports for ssp. *simplex* were diploid. The 19 reports for diploids from Alaska and western Canada (Table 1) further confirm that ssp. *simplex* is diploid.

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J. C. S. AND C. X.
DEPARTMENT OF BIOLOGY
UNIVERSITY OF WATERLOO
WATERLOO, ONTARIO
CANADA N2L 3G1

J. G. C.
BIOLOGY DEPARTMENT
SLIPPERY ROCK UNIVERSITY
SLIPPERY ROCK, PA 16057 U.S.A.

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A FLORISTIC AND VEGETATION ANALYSIS OF A FRESHWATER TIDAL MARSH ON THE MERRIMACK RIVER, WEST NEWBURY, MASSACHUSETTS[1]

FREDRICKA ANN CALDWELL AND GARRETT E. CROW

ABSTRACT

Plant community structure and selected physical parameters influencing vegetational patterns were studied in a Merrimack River freshwater tidal marsh. A flora of 88 vascular plant species was documented. Special consideration was given to three species, *Scirpus fluviatilis, Bidens eatonii* and *Eriocaulon parkeri,* listed as rare for the Commonwealth of Massachusetts. Species abundance data were used to classify the vegetation into eight plant cover types using the computer program TWINSPAN.

Key Words: Freshwater tidal marsh, plant community, plant classification, TWINSPAN, rare plants, northeastern Massachusetts

INTRODUCTION

Freshwater tidal marshes develop in coastal rivers flooded daily by the incoming tides. The advancing salt front produces a salinity gradient from the ocean upstream to that portion of the river no longer under tidal influence. Coastal wetlands along this gradient are classified on a salinity-based system which defines a freshwater tidal marsh as one with an average annual salinity of less than 5‰ (parts per thousand) (Odum et al., 1984). These freshwater or near-freshwater conditions occur because the tidal influence exceeds the advance of the underlying salt wedge, causing a backflow of the overlying freshwater into the marshes. Freshwater tidal marshes occur where the salt front reaches its upstream limit in late summer when the river discharge is low.

The fluctuating physical conditions induced by changing tides make a freshwater tidal marsh a unique environment for vegetation. Several studies have been conducted describing the distribution and abundance of intertidal vascular plants from these marshes (Nichols, 1920; Fassett, 1928; Ferren and Schuyler, 1980; Metzler and Rosza, 1982; Odum et al., 1984; Odum, 1988). Fresh-

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water tidal marshes have been described by several authors as transition zones between fresh and salt water habitats (Philipp and Brown, 1965; Anderson et al., 1968; Ferren, 1976; Garofalo, 1980; Haramis and Carter, 1983), and species diversity across this transition zone typically decreases as salinity increases (Odum, 1988). A number of unusual species restricted to estuaries, as well as rare plants, have been documented from this type of marsh (Fernald, 1903; Fassett, 1925a, 1925b, 1928; Mathieson and Fralick, 1973; Ferren and Schuyler, 1980; Crow, 1982; Sorrie, 1987; Barrett, 1989 MS thesis, Univ. of Conn., Storrs, CT).

The forces of strong tidal and river currents and ice floes have a strong influence on the morphology and vegetation of a freshwater tidal marsh. Marsh soil is directly affected by sediment accretion and erosion as well as by other factors (Ahnert, 1960; Dionne, 1968, 1969, 1974; Garofalo, 1980; Serodes and Troude, 1984).

Zonal patterns of vegetation may develop in response to environmental gradients in freshwater tidal marshes. Some studies have correlated plant community structure and productivity with certain environmental parameters such as elevation of the marsh, tidal submergence, salinity, soil texture, soil organic material and soil redox potential (Disraeli and Fonda, 1979; Hutchinson, 1982; Ewing, 1983, 1986).

Freshwater tidal marshes occur on both coasts in North America, but the Pacific coast marshes are not as extensive as those along the Atlantic (Disraeli and Fonda, 1979). In Massachusetts, two river systems support sizable freshwater tidal marshes, the North River (Plymouth Co.) and the Merrimack River (Essex Co.). The Merrimack River arises in the White Mountains of New Hampshire and empties into the ocean near Newburyport, Massachusetts, where the Merrimack forms a wide estuary at its confluence with the Parker River, north of Plum Island.

This study of the Merrimack River freshwater tidal marsh was initiated with the following objectives: 1) to conduct a complete floristic survey of the area; 2) to collect species abundance data and classify the vegetation into cover types; 3) to document populations of plants listed as rare for the Commonwealth of Massachusetts; 4) to describe the marsh habitat, including plant cover types, tidal fluctuation, free water salinity, and soil organic matter content; and 5) to assess the relationship between plant community structure and selected environmental characteristics.

Site Description

The study site occurs along a segment of the Merrimack River in the Town of West Newbury, Essex County, Massachusetts, approximately nine miles from the ocean (42°49′N Lat., 71°57′W Long.). The study area begins at the Indian River and extends east for 1¼ miles to the Artichoke River. Three marsh areas occur between these two tributaries, separated by sections of rocky shoreline (Figure 1). The average area of each marsh is approximately 400 × 150 meters.

Because the high tide zone borders a sloping forested riverbank, the Merrimack River marsh contains only two small areas where high marsh habitat has developed. These areas occur as slightly elevated islands near the mouths of the Artichoke and Indian Rivers, and appear to be sections of land that have become isolated by a backwash of these tributaries from tidal flooding.

MATERIALS AND METHODS

Environmental Measurements

Tidal Amplitude

Tidal amplitude was recorded during September and October of 1989 using a Stevens Model F Recorder. Since the Merrimack River is used extensively for boating, it was not advisable to place the recorder in the river channel at the low tide level. A reference location was chosen for the recorder platform in Area #3 (see Figure 1) at the edge of the vegetation nearest the river channel at low tide. Therefore, data do not include full low tide range of the river, but they do measure tidal amplitude and duration of flooding for all vegetation zones in the marsh.

Surface elevation of this marsh area relative to the recorder platform was measured using a line level and meter rod. The longest transect in the center of Area 3 was chosen to represent the average elevation of sampled areas.

Salinity

Free-water salinity measurements were taken in the spring and fall of 1989 using a portable Y-S-I model 33 salinometer. Mea-

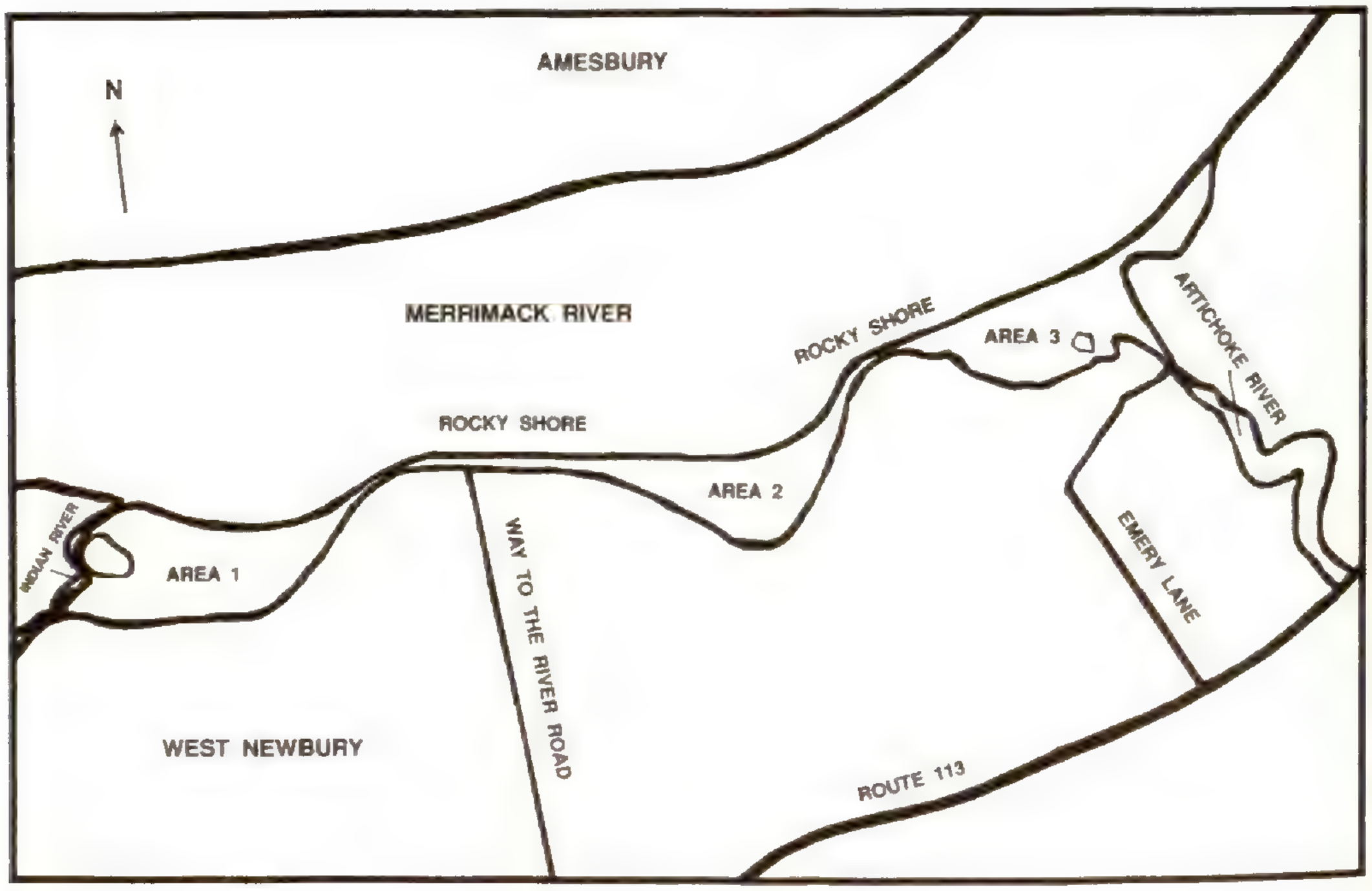

Figure 1. Map of study site.

surements were recorded during the high tide cycle at several sampling stations in the marsh and at various depths within the water column. Temperature and conductivity were also recorded.

Soil Organic Matter Content

Soil samples were collected in June 1989 from Area #1 for organic matter content determination. Three replicates were collected at 5 cm and 10 cm depths at four intervals along a transect corresponding with different plant cover types. Samples were oven-dried at 80°C for 24 hours and ashed in a muffle furnace at 475°C for 24 hours. Percentages of water and organic matter content of the soil were calculated from these weights.

Vegetation Analysis

Vegetation data were collected in August and September of 1988 and 1989. These months were chosen for vegetation sampling because combined patterns of all species produce a peak community biomass in August (Doumlele, 1981). Sampling was done using the stratified random sampling method (Mueller-Dombois and Ellenberg, 1974). Three transects were established

in each of the three marsh areas, and 23 transects were established along the rocky shore areas at 50-meter intervals for a total of 32 transects. Each transect ran perpendicular to the edge of the river and extended from the beginning of the rooted vegetation exposed at low tide to the upper edge of the high tide zone. A quadrat size of ½ × ½ meter was used in a total of 323 sample plots. One quadrat was randomly located within each five meter segment of marsh transect and three meter segment of rocky shore transect. A shorter random sampling segment was chosen for the rocky shore transects because the length of each of these transects was relatively short, and elevational gradient was steeper.

Percent cover was recorded to estimate the abundance of 30 vascular plant species occurring in the quadrats. Cover was defined as the projection of the crown or shoot area of a species to the ground surface expressed as a percent of the quadrat area (Mueller-Dombois and Ellenberg, 1974).

Data were analyzed using TWINSPAN (Two-Way Indicator Species Analysis), a Fortran program designed to construct a classification of samples that are then used to classify species according to their ecological preference (Hill, 1979). The program groups quadrat samples and species by repeated dichotomies. Three ordinations are used in the dichotomy determination: 1) primary ordination, which uses a reciprocal averaging method; 2) refined ordination, which uses differential species; and 3) indicator ordination, which uses indicator species (Hill, 1979).

Floristics

An inventory of the vascular plants of the Merrimack River freshwater tidal marsh was undertaken during the 1988 and 1989 field seasons. Voucher specimens were collected and deposited at NHA. Documentation of three rare plants, *Bidens eatonii, Eriocaulon parkeri* and *Scirpus fluviatilis* and their habitat description were also included in this study.

Identifications were based on *Aquatic and Wetland Plants of Northeastern North America* (Crow and Hellquist, in press), *A Manual of Vascular Plants of Northeastern United States and Adjacent Canada* (Gleason and Cronquist, 1963) and *Gray's Manual of Botany* (Fernald, 1950). Additional references included: *New Britton and Brown Illustrated Flora* (Gleason, 1952) and

Aquatic Vascular Plants of New England Parts 1–8 (Hellquist and Crow, 1980, 1981, 1982, 1984; Crow and Hellquist, 1981, 1982, 1983, 1985).

RESULTS AND DISCUSSION

Environmental Measurements

Tidal Amplitude

The total range of tidal amplitude measured for 76 cycles was 0–150 cm, with high tides ranging from 82–150 cm; mean high tide calculated from all recorded tides was 115 cm.

The elevation of the marsh surface was 40 cm, as measured from the base of the tide gauge to approximately mean high tide along a 147 meter transect. A rise in elevation of 15 cm occurred along the first 25 m nearest the river; the remaining 25 cm of rise in elevation occurred over the last 122 m of the marsh. This gradual slope across the marsh platform is typical of freshwater tidal marshes, and has been described by several authors (Metzler and Rosza, 1982; Ewing, 1983; Odum et al., 1984; Mitsch and Gosselink, 1986).

Many sections of the high tide zone end in an erosional step that abuts a sloping river bank. This step accounts for much of the difference in high tide water levels and the measured slope of the marsh surface. A similar geomorphology was reported by Hutchinson (1982) in the Fraser River tidal marshes of British Columbia. Other sections end in a forested slope which was beyond the scope of this study.

Duration of inundation in the Merrimack River marsh at the elevation of the tide gauge was approximately 16 hours per day during two tide cycles. Mean high tide data (115 cm) were used for this determination. Water level plotted against duration of inundation at the plant/soil interface shows submergence time for different elevations across the marsh platform (Figure 2). Cover types such as *Scirpus pungens* and *Spartina alterniflora* that occur at the lower edge of the vegetation zone are partially submerged for 16 hours a day and fully submerged for a portion of that time, depending on their height and elevation. Decreased levels of light and gas exchange, characteristic of a submerged

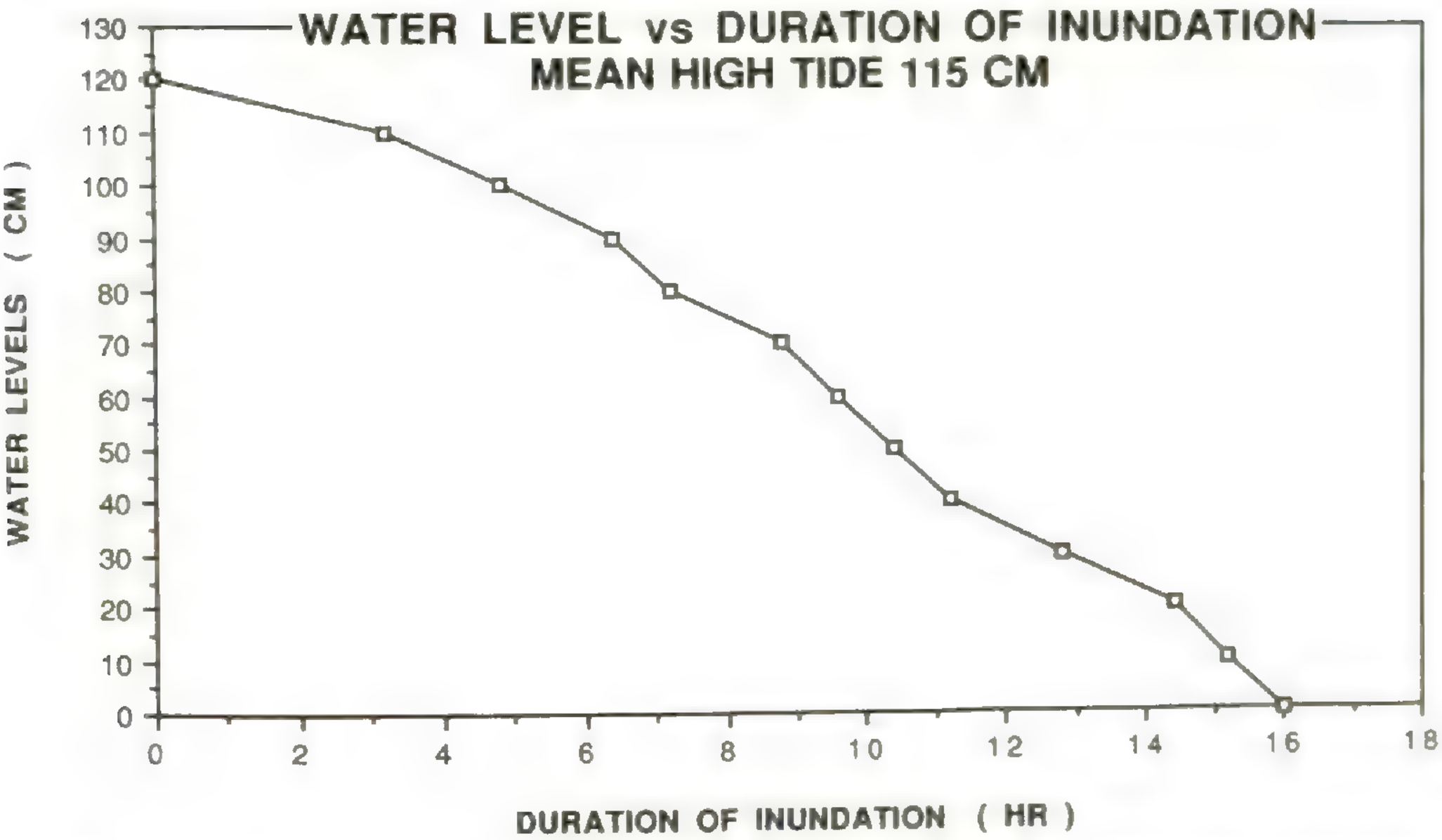

Figure 2. Water level versus duration of inundation at the plant/soil interface for two tide cycles taken from 115 cm mean high tide data.

habitat, make this environment suitable for only a select number of emergent plants.

The mid-marsh and backmarsh portions of the surface below 40 cm elevation are flooded for at least 11 hours per day at the plant/soil interface (Figure 2). Cover types occurring in this area include *Scirpus tabernaemontanii*-type, *Acorus calamus*-type and *Zizania aquatica*-type. Although tide gradient front-to-back in the marsh seems relatively small, it is probably a significant factor in controlling distribution of these cover types.

In a study based on a linear regression analysis of selected physical parameters in the Nooksack River delta in Bellingham Bay, Washington, Disraeli and Fonda (1979) reported that the most important environmental factor affecting plant distribution was elevation above mean low water. They further added that this factor controlled frequency and duration of submergence and indirectly affected all other factors. Using analysis of variance to assess which physical factors governed plant species distribution. Hutchinson (1982) reported that "species distribution is clearly controlled by the elevation of the marsh platform and the associated tidal regime." Several other authors report similar conclusions (Johnson and York, 1915; Nichols, 1920; Philipp and Brown, 1965; Metzler and Rosza, 1982; Ewing, 1983; Keddy, 1983; Chabreck, 1988).

Table 1. Water analysis data recorded from eight stations at high tide in the Merrimack River marsh study site.

Date 1989	Average Salinity (‰)	Salinity Range (‰)	Average Conductivity (μmho)	Average Temperature (°C)	Average Temperature (°F)
May 20	0.0	—	—	20	68
June 18	0.0	—	106	20	68
Sept 16	1.4	0.8–4.8	1742	21	70

Salinity

Except for one sampling period in the fall, all samples showed 0‰ salinity. The only detectable salinity occurred in mid-September, when it averaged 1.4‰ in the water column with a range of 0.8 to 4.8‰ (Table 1). These readings classify the study site as a freshwater tidal marsh, since by definition, this type of marsh must be tidal and have an average annual salinity of less than 5‰ (Odum et al., 1984).

The seasonal salinity pattern reported here supports previous data recorded from this area of the Merrimack River. Jerome et al. (1965) reported that during an eight month survey only one salinity measurement of 5.0‰ was recorded in October from the Artichoke River Station in the Merrimack River.

In another study conducted on the Merrimack River, Miller et al. (1971) indicated that the limit of the salt intrusion at high tide varied from 4.3 to 10.9 miles from the mouth depending upon the season. They found gross fluctuations in salinity both daily and seasonally in this section of the river. Disraeli and Fonda (1979) also found a similar salinity pattern in the Nooksack River in Bellingham Bay, Washington, with a maximum salinity of 5.19‰ in October.

Soil Organic Matter Content

Soil organic matter and water content measurements may help to determine the nature of the marsh soil, which varies considerably among river systems and marsh types (Chabreck, 1988). Soil samples for these determinations were collected; organic matter analysis showed a gradient from 1.49 percent in the low tide zone to 19.81 percent in the backmarsh (Table 2). This type of

Table 2. Soil analysis data taken at four intervals and at two depths along a transect in Area 1. These data represent an average of three samples.

Distance from Vegetation Edge (Low Tide Zone) (Meters)	% Organic Content of Soil		% Water Content of Soil	
	Depth		Depth	
	5 cm	10 cm	5 cm	10 cm
5	1.64	1.49	26.73	20.95
25	2.46	2.57	30.89	25.78
75	6.85	4.29	43.66	33.17
125	19.81	17.86	68.09	64.41

gradient is predictable since the action of the tides sweeps away the organic debris from the low- and mid-marsh areas and deposits it in the backmarsh. Whigham and Simpson (1975) also found that soil organic concentration increased on a gradient from actively flooded stream banks to less actively flooded areas in the Hamilton Marshes in New Jersey.

The soil in the Merrimack River foremarsh is mainly gray clay mixed with some silt and sand. Since the organic content of this soil is less than 15 percent, it may be classified as a mineral soil (Dachnowski-Stokes, 1940). By contrast, the backmarsh substrate can be classified as muck since it contains an organic content in the 15 to 50 percent range. Large deposits of silt are also an important component of the mid- and backmarsh soils.

Although a great deal of between- and within-site variability exists, average organic content taken from a series of samples from the east coast of North America ranged from 20 to 70 percent, with a mean of 35 percent (Odum, 1988). Along the Delaware River in New Jersey, Whigham and Simpson (1975) showed a range of 14 to 40 percent organic matter. Relative to these findings, the Merrimack River marsh has a low organic content. These results may be due to the absence of "high marsh" areas relative to other freshwater tidal marshes. High marsh areas are elevated sections of the marsh that are less exposed to tidal currents. They are usually flooded only during seasonal high tides and, for a variety of reasons, poorly drained. These conditions facilitate the build-up of organic matter in the soil. The low measurement may also be a result of insufficient sampling.

Water content in the Merrimack River marsh tends to parallel organic content. A front-to-back marsh gradient exists with re-

spect to soil water content, with a range of 27 percent to 68 percent respectively (Table 2). Both Disraeli and Fonda (1979) and Hutchinson (1982) found that soil water content was highest in the high- and mid-marsh areas at low tide. They attribute these findings to differences in soil texture and drainage patterns from front to backmarsh. There is usually a higher proportion of fine sand in low marsh substrate, resulting in a more rapid drainage of these soils during ebb tide.

In contrast, the backmarsh contains a more organic matter and drainage patterns are poorer. In the Merrimack River marsh, backmarsh is typically waterlogged due to gradual surface slope and dense network of rhizomes of *Acorus calamus* in the mid-marsh section.

Differences in percent organic and water content between 5 cm and 10 cm depths are shown in Table 2. In all cases, percent organic matter and water content decreased with depth. The dynamics of an intertidal marsh prevent long-term accumulation of organic matter, and consequently less is found at greater depths.

Plant Cover Types

The vegetation was classified using TWINSPAN into eight plant cover types (Figure 3). Four hierarchical divisions were used to cluster the 323 quadrats and 30 plant species into these eight groups.

In the first dichotomy, TWINSPAN separated the 66 quadrats corresponding to the rocky shore sites from the 257 marsh quadrats. Five plant cover types were further delineated from the analysis of marsh vegetation data and were named according to their dominant vascular plant species. The *Spartina alterniflora* cover type is the first to be defined on the second divisional level. The *Scirpus tabernaemontanii* and *Acorus calamus* cover types are split on the third divisional level, but they are not completely defined until they are separated from the *Sagittaria graminea* and *Zizania aquatica* cover types on the fourth divisional level. Divisions with less than five quadrats are not considered sufficiently distinct to designate as a cover type.

In the rocky shore areas, three plant cover types are recognized at three divisional levels, *Spartina pectinata* cover type at level two and *Scirpus pungens* and *Amaranthus cannabinus* cover types at level three (Figure 3). Fewer quadrats were sampled in the

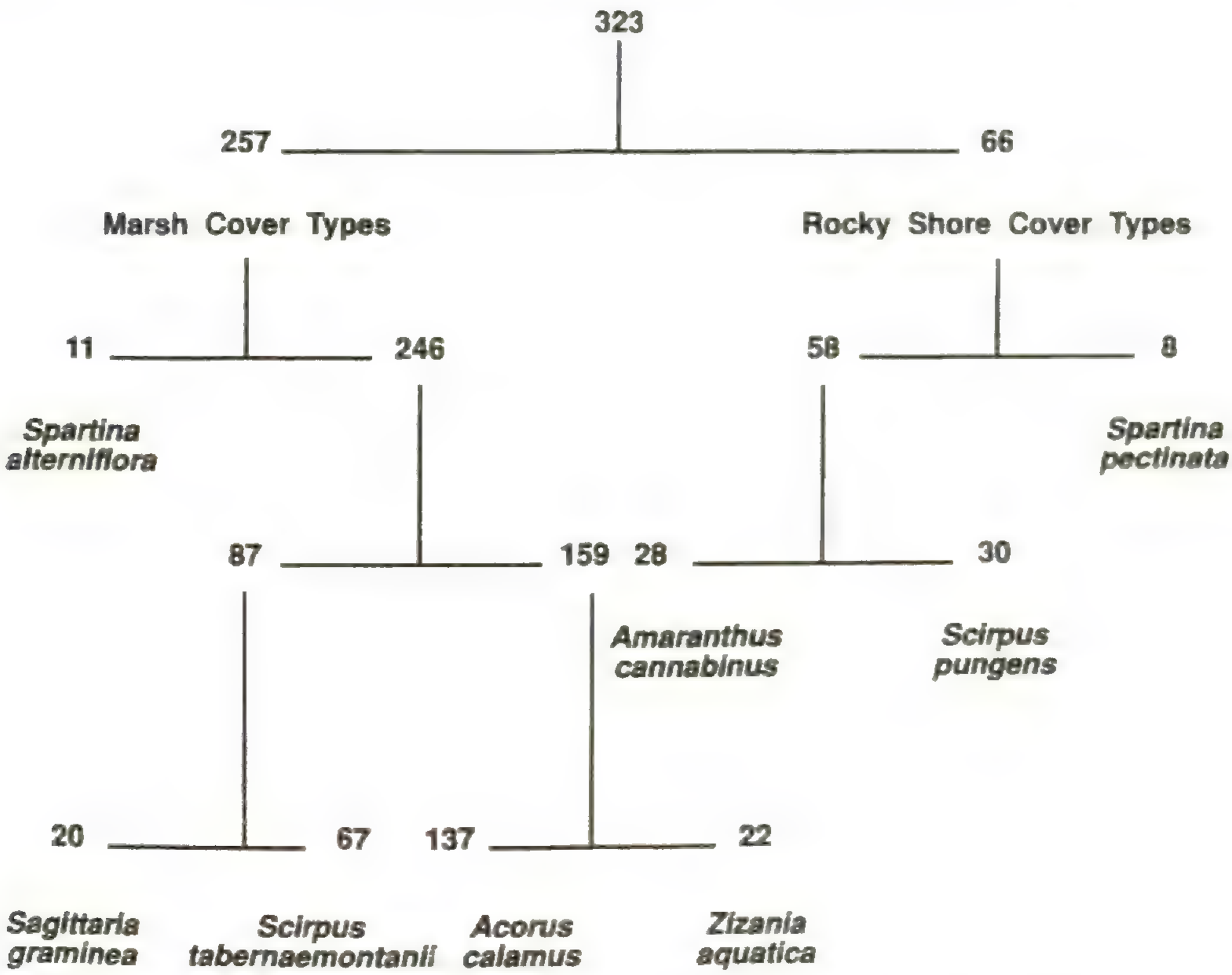

Figure 3. TWINSPAN analysis showing the eight plant cover types classified at four hierarchical levels.

rocky shore sites since these areas comprised a considerably smaller portion of the study site than the three large marshes. Because of the comparatively small number of samples and sparseness of vegetation, it is not meaningful to describe cover types beyond the third divisional level in these areas.

The two habitats identified by the first dichotomy exhibit differences in topography, substrate and vegetational patterns. The three marsh areas are broad with sections of dense vegetation, a relatively flat surface and a silty-clay organic substrate. Borders of these marshes adjacent to the river channel consist of extensive mud flats that are exposed at low tide and are devoid of vegetation throughout the year. The overriding impression of the vegetational pattern in these marsh areas is one of zonation due to broad bands of dominant species, although the borders may be highly irregular (Figure 4).

In contrast, rocky shoreline areas which occur between marshes are characterized by more steeply sloping surfaces, stony-sandy substrates and mosaic patterns of sparse vegetation (Figure 5).

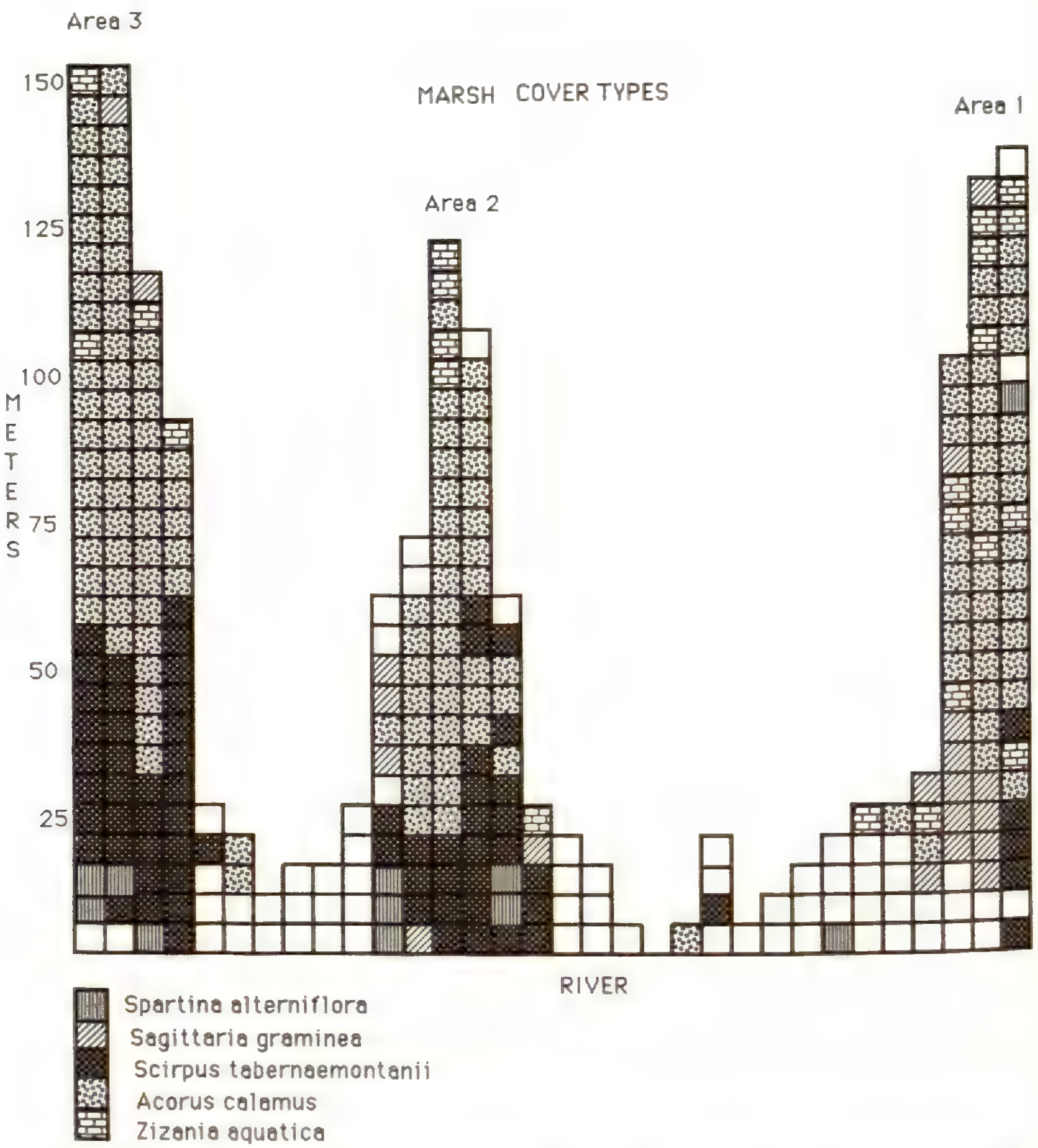

Figure 4. The distribution of marsh cover types in three marsh areas. Each square represents a ½ × ½ meter quadrat within a 5-meter segment of transect. The transects are depicted vertically and are separated horizontally by distances ranging from 50–150 meters.

These shore areas are more exposed to erosive currents, ice scouring, and wind than are the marshes, and this high degree of disturbance may be a contributing factor to the patchy distribution of vegetation. While each cover type throughout the marsh is characterized by one or more dominant plants, some species such as *Polygonum punctatum* and *Sagittaria latifolia* do not have a strong affinity for any particular area within the intertidal zone, and are found in several different cover types.

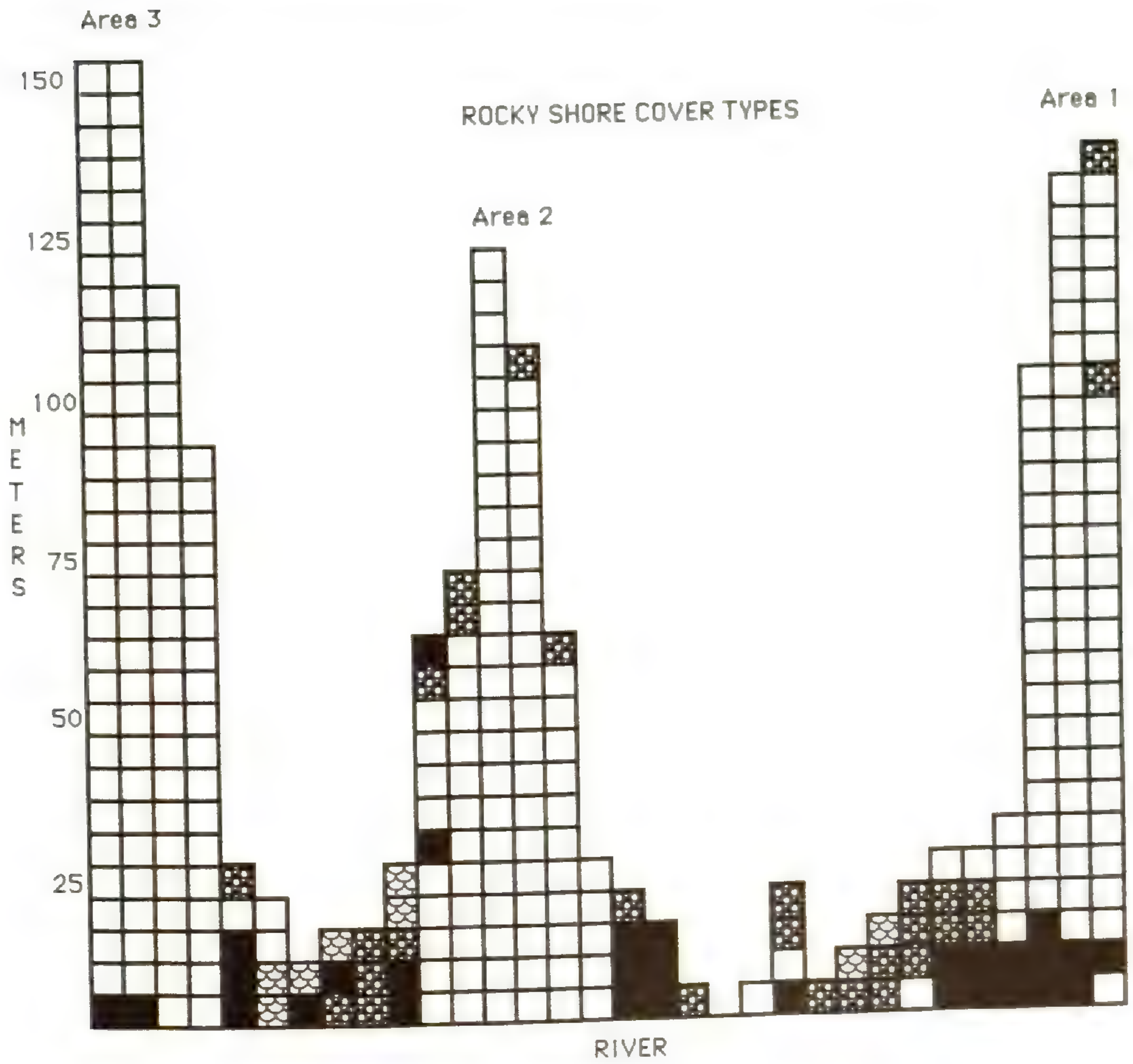

Figure 5. The distribution of rocky shore cover types. Each square represents a ½ × ½ meter quadrat within a 3-meter segment of transect. The transects are depicted vertically and are separated horizontally by distances ranging from 50–150 meters.

MARSH PLANT COVER TYPES

Spartina alterniflora Cover Type

The *Spartina alterniflora* cover type is one of the less common of the eight plant associations described. The community can be characterized by three species, but *Spartina alterniflora* dominates, with a mean cover of 26 percent (Table 3).

Spartina alterniflora is typically found in more saline habitats, but since freshwater tidal marshes are transitional to salt marshes,

Table 3. Mean percent cover for 25 species in 8 plant cover types. 1 = *Spartina alterniflora*. 2 = *Sagittaria graminea*. 3 = *Scirpus tabernaemontanii*. 4 = *Acorus calamus*. 5 = *Zizania aquatica*. 6 = *Spartina pectinata*. 7 = *Amaranthus cannabinus*. 8 = *Scirpus pungens*. (Species with <1% cover are omitted.)

Cover Types	1	2	3	4	5	6	7	8
Number of Quadrats	11	20	67	137	22	8	28	30
Sagittaria graminea	—	38	2	2	4	—	1	2
Ludwigia palustris	—	—	—	—	1	—	—	—
Elodea nuttallii	1	—	3	1	—	—	—	—
Zizania aquatica	—	7	—	—	42	—	1	—
Spartina alterniflora	26	—	—	—	—	—	—	—
Scirpus tabernaemontanii	9	9	32	1	—	—	—	—
Elatine americana	—	—	5	—	—	—	—	—
Sagittaria latifolia	—	2	2	10	1	—	1	—
Acorus calamus	—	1	13	55	3	—	1	—
Bidens cernua	—	3	—	3	13	—	—	—
Pontederia cordata	—	—	—	6	3	—	—	—
Scirpus fluviatilis	—	—	—	3	2	—	—	—
Polygonum punctatum	—	1	—	2	3	4	2	—
Bidens sp.	—	—	—	2	13	—	2	—
Sium suave	—	—	1	5	3	14	9	—
Lythrum salicaria	—	—	—	—	—	3	—	—
Spartina pectinata	—	—	—	—	—	39	—	—
Lycopus americanus	—	—	—	—	—	1	—	—
Aster novi-belgii	—	—	—	—	—	9	—	—
Amaranthus cannabinus	—	—	—	—	—	3	16	—
Pilea pumila	—	—	—	—	—	—	1	—
Juncus acuminatus	—	—	—	—	—	—	1	—
Eleocharis smallii	—	1	—	—	1	—	1	—
Mimulus ringens	—	—	—	—	—	—	1	—
Scirpus pungens	—	2	—	—	—	5	6	17

this saltwater cordgrass may occasionally be found upstream under nearly freshwater conditions (Ferren, 1976). In the Merrimack River marsh, *Spartina alterniflora* is most abundant at the seaward edge of the study site in the low tide zone. A dense network of rhizomes and roots makes it very resistant to erosive forces, allowing it to colonize unstable areas (Garofalo, 1980). Although *Scirpus tabernaemontanii* grows with these clumps of cordgrass, it is usually found in the midmarsh areas where it forms nearly homogenous zones. The other components of this cover type, such as *Elodea nuttallii* and *Elatine americana*, are submerged aquatics that are tolerant of the alternately flooded and exposed mud flats in the low tide zone.

Sagittaria graminea Cover Type

The *Sagittaria graminea* cover type (Table 3) extends from exposed mud flats in the low tide zone to fringes of the backmarsh. The dominant species, *Sagittaria graminea,* is typically associated with *Scirpus pungens* and *Scirpus tabernaemontanii* in the low- to mid-marsh areas, and with *Zizania aquatica, Sagittaria latifolia, Bidens cernua* and *Polygonum punctatum* in the backmarsh. This distribution occurs primarily because *Sagittaria graminea* has adapted to a wide range of environmental conditions.

When *Sagittaria graminea* occurs in the low tide zone where it is submerged throughout most of the day, the plants form colonies of sterile rosettes with linear-lanceolate phyllodia. In the backmarsh, however, the plants are only occasionally submerged, and it is under these conditions that they develop larger, broader leaf blades and occasionally flowers. Ferren and Schuyler (1980) reported that plants of the upper intertidal zone had several verticils on their inflorescence axes, while those growing in the lower intertidal zone had one to rarely three verticils of flowers. Flowering specimens of *S. graminea* in the Merrimack River marsh usually had one or two verticils. *Sagittaria graminea* rarely produces achenes in New England (Hellquist and Crow, 1981), and none was observed in this study.

Scirpus tabernaemontanii Cover Type

This cover type is characterized by the soft-stemmed bulrush, *Scirpus tabernaemontanii* (Table 3), which forms a broad band from the lower edge of the vegetation zone to the midmarsh area. Other rhizomatous perennials such as *Acorus calamus* and *Sagittaria latifolia* are included in this association, but they rarely inhabit the low tide zone. The submerged aquatics, *Elodea nuttallii* and *Elatine americana,* grow intermixed with these emergents and form small patches on the surface of the mud in frequently inundated areas. This cover type is found mainly at sites with a silty clay substrate, and its borders are abrupt when the substrate changes to sand and gravel near the rocky shore areas.

The dominant species in this cover type, *Scirpus tabernaemontanii,* is a rapidly growing perennial which reaches heights of three meters or more. Stored nutrients in the rhizomes may allow

the early and rapid development of plants of this species that obtain their peak biomass in early June along with *Acorus calamus* (Whigham et al., 1978). The height, abundance and early emergence of *S. tabernaemontanii* make it one of the predominant species of the entire freshwater tidal marsh.

Acorus calamus Cover Type

The *Acorus calamus* cover type spans by far the largest area of the Merrimack River marsh, extending from midmarsh to the border of the backmarsh in some sections. The TWINSPAN analysis clustered 137 quadrats and 11 species in separating out this community. Because this cover type encompasses such a large area and tidal range, its species diversity is relatively high, despite the overriding dominance of *A. calamus* (Table 3). Dense rhizomatous colonies of this plant dominate the midmarsh section and may extend up to sixty meters along certain transects. Apparently this species reproduces almost exclusively by rhizomes since it is a common plant in these marshes and has not been documented in several seed bank surveys (Leck and Graveline, 1979; Leck and Simpson, 1987; Simpson et al., 1983).

The backmarsh elements of this cover type are characterized by the broad-leaved emergents *Sagittaria latifolia, Pontederia cordata,* and occasionally *Peltandra virginica.* These species are most abundant in wet organic mucky substrates. Although *Sagittaria latifolia* also occurs in the midmarsh, plants are larger and flower more frequently in the backmarsh. *Scirpus fluviatilis* is another important member of this backmarsh cover type, and is discussed in the rare plant section.

The annual plant component of this cover type is found most often intermixed with *Acorus calamus.* The dense and partially exposed system of rhizomes of *A. calamus* gives the marsh an irregular surface which provides a microhabitat for seeds of annuals such as *Sium suave, Bidens cernua, B. connata,* and *B. eatonii.* In winter, clumps of these rhizomes are uplifted along with ice blocks and deposited downstream along the shoreline (Hardwick-Witman, 1984 MS thesis, Univ. of New Hampshire, Durham, NH). Observations over the two year-study period, however, revealed that erosive forces prevented establishment of these clumps in the low tide zone in the Merrimack River marsh.

Zizania aquatica Cover Type

This cover type consists of several perennial backmarsh emergents, but it is dominated by the late-summer annuals *Zizania aquatica* and *Bidens* spp. *Zizania aquatica* requires soft mud and slowly circulating water typical of a backmarsh habitat (Odum et al., 1984), but it may also be found in small depressions throughout the midmarsh (Figure 4). Other associated species include *Sagittaria graminea, Pontederia cordata, Polygonum punctatum, Sium suave, Ludwigia palustris* and *Eleocharis smallii* (Table 3).

The late maturity of *Zizania aquatica* and *Bidens* makes this cover type the last to appear in the seasonal succession of marsh vegetation. Root growth predominates during early development of *Z. aquatica,* but later in the season, shoot growth may be up to 6.5 cm per day (Good and Good, 1975); this shallow-rooted grass can reach heights of 4 m. Lodging of large stands of this plant has been observed in the study site due to waves from storms and heavy boat activity on the river.

ROCKY SHORE COVER TYPES

Spartina pectinata Cover Type

This freshwater cordgrass cover type represents a small portion of the rocky shore vegetation. Its definition by TWINSPAN involved only eight quadrats. *Spartina pectinata,* the dominant species in this cover type, occurs most often along back borders of rocky shore areas in sandy substrate with other species such as, *Aster novi-belgii* and *Lythrum salicaria.* It also grows mixed with annuals that are common there (Table 3). The two major perennials in this cover type, *Spartina pectinata* and *Aster novi-belgii,* have rhizomatous root systems that enable them to withstand the adverse conditions characteristic of this section of the Merrimack River marsh. This band of shoreline is one of the most highly disturbed areas since it is often filled with debris that is shifted back and forth along the shoreline with each changing tide.

Amaranthus cannabinus Cover Type

The *Amaranthus cannabinus* cover type is the most diffuse of the eight described. It occurs most often in the rocky shore areas,

but may be found occasionally in backmarsh areas where the substrate is firm and gravelly (Figure 5). In rocky shore areas, this cover type extends from low-to-high tidal elevations, without an apparent zonal pattern.

Since the *Amaranthus cannabinus* cover type is comprised mainly of annuals (Table 3), abundance of the different species may change dramatically from year to year. Leck and Graveline (1979) found that annuals comprised seven of the ten most numerous species encountered in seed bank experiments conducted in the Hamilton freshwater-tidal marshes on the Delaware River near Trenton, New Jersey. They further reported that the riverbank, which had been scoured of all vegetation by ice and waves during the winter, produced dense growths of annuals during the summer. In the Merrimack River marsh, these rocky shore areas occur around two points that project into the river and are highly exposed to wind and waves (Figure 1). These extremely disturbed sites provide an open habitat for fast-growing annual species, with the rocky substrate affording the seeds protection from river and tidal currents. Backmarsh occurrence of the *Amaranthus cannabinus* cover type may be due to similar stony substrate in these areas.

Scirpus pungens Cover Type

Scirpus pungens dominates this cover type, intermixing only occasionally with patches of *Sagittaria graminea* (Table 3). *Scirpus pungens* forms a nearly monospecific zone in the low tide mud flats or occurs as scattered populations throughout the rocky shore areas (Figure 5). The mean cover value of other species associated with this cover type is less than 1 percent. When this small-stemmed perennial colonizes the lower limit of the low tide zone, it is submerged throughout most of its life. In the spring, the cold temperature of the mud and overlying river water delay shoot emergence until mid-May, a time when *Acorus calamus* is already beginning to flower. These plants remain somewhat stunted throughout most of the growing season and rarely produce flowers. Deschenes and Serodes (1985) found that *Scirpus pungens* (cited as *Scirpus americanus*) can withstand nearly 100 percent submersion under freshwater conditions, but its population size declines with increasing salinity.

Scirpus pungens matures relatively rapidly on the more elevated sections of rocky shore areas, however, and flowers in early June. This is one of the few rhizomatous plants that colonizes sloping surfaces and stony substrates of the Merrimack River shore areas. Hutchinson (1982) and Odum (1988) considered this species to be a pioneer, capable of quickly colonizing disturbed or bare areas by seed dispersal.

RARE PLANT DOCUMENTATION AND HABITAT DESCRIPTION

Three plant species listed by Sorrie (1987, 1990) as rare for the Commonwealth of Massachusetts occur in the Merrimack River marsh, including *Scirpus fluviatilis* (special concern), *Eriocaulon parkeri* (endangered) and *Bidens eatonii* (threatened). *Scirpus fluviatilis* has a wide distribution in fresh and tidal rivers across the United States. *Eriocaulon parkeri* and *Bidens eatonii* are confined to estuaries along the east coast (Crow and Hellquist, in press; Hellquist and Crow, 1982).

Six current sites have been documented for *Scirpus fluviatilis* in Massachusetts, including the Merrimack River freshwater tidal marsh (Sorrie, pers. comm.). These plants occur most often in the middle and backmarsh areas of the study site, rooted in a muddy, silty substrate and growing on the slightly elevated borders of islands in the marsh. Although large stands develop, most plants lack inflorescences, and reproduction is almost exclusively vegetative by means of an extensive rhizome system. Ferren and Schuyler (1980) reported similar observations of *S. fluviatilis* populations along the Delaware River. Leck et al. (1988) also reported that although this species occurred in their study area, it was not represented in the seed bank survey nor in the field as seedlings; they concluded that it rarely reproduces by seeds.

The second rare plant, *Eriocaulon parkeri*, is reported in only four locations in Massachusetts, including the Merrimack River marsh (Hellquist and Crow, 1982; Sorrie, pers. comm.). One small population was documented near the west end of the study site, and a second population, reported further down river, could not be located. Three boat docks have been built out from the riverbank, and a large section of shoreline clearing occurred during the two years of this study; this activity may account for disappearance of the second population.

The estuarine pipewort, *Eriocaulon parkeri,* grows in a gravelly, sandy substrate on the upper slope of the rocky shore in open sunlight. These plants are submerged for ca. 11 hours a day at high tide; the substrate in this area, although sandy, appears to remain continuously wet even at low tide. Associated vegetation is sparse, consisting of species such as *Scirpus smithii, Cyperus bipartitus, Isoetes echinospora, Equisetum fluviatile, Ludwigia palustris* and *Lindernia dubia.*

Although the range of *Eriocaulon parkeri* extends from Maine to South Carolina in estuaries along the coast, it is listed as rare and endangered for New England, Maine, Massachusetts and Connecticut (Crow et al., 1981; Hellquist and Crow, 1982). It is also rare in Delaware, New Jersey and New York (Tucker et al., 1979; Mitchell et al., 1980; Snyder and Vivian, 1981). Efforts should be made to protect the remaining populations of this rare plant and to preserve its habitat. The Merrimack River site is especially vulnerable due to recent and potential marsh destruction.

The third rare plant species, *Bidens eatonii,* was discovered by Alvah A. Eaton in 1902 from the "brackish shores of the Merrimack River in Newburyport, Massachusetts" (Fernald, 1903), just downstream from the study area. Since then, eight weakly defined varieties have been described, four of which have been documented from the Merrimack River estuary, var. *eatonii* Fern., var. *fallax* Fern., var. *illicita* Blake and var. *kennebecensis* Fern. (Fassett, 1925a; Sherff, 1937). In addition to these varieties, three other species of *Bidens* also occur in the study site, *B. cernua, B. frondosa* and *B. connata.*

Since *Bidens cernua* has simple sessile leaves and *B. frondosa* has compound petiolate leaves, both are easily recognized in the field. However, *Bidens eatonii* and *B. connata* are very similar and have simple petiolate leaves that frequently have basal lobes, and flowers that typically lack ray florets. In many cases it was impossible to distinguish between these two species in the field, especially since they were in the vegetative stage at the time of vegetation sampling. Therefore, these two species were grouped together in the abundance data for vegetation analysis.

Characters that have been considered important in distinguishing these two species include number, size and shape of terminal heads, as well as the surface features of achenes. *Bidens connata* has large (30–60 flowers) rounded heads, and *B. eatonii* has small-

er (8–30 flowers) campanulate heads (Fassett, 1925a, 1925b). However, in examining many petiolate, simple-leaved specimens of *Bidens* in the Merrimack River marsh, a range of terminal head sizes and shapes was observed. Sorrie (1987) also found similar intermediate head characters in plants from a Threemile River population in Bristol Co., Massachusetts.

Achene surface features such as striations and tubercles also proved to be unsatisfactory as distinguishing characters. Both species have striate achenes (Fassett, 1925b) and the presence of tubercles, often used to distinguish *B. connata* from *B. eatonii,* was reported by Fernald (1908) to be an inconstant character.

Taxonomic identity could be further complicated in that all four species commonly grow together on tidal shores and in brackish marshes, and hybrids have been reported to occur between some of them. Fassett (1925a) described *B.* × *multiceps,* a hybrid of *B. connata* and *B. eatonii* from the Taunton River estuary of Massachusetts. Also, in a study of *Bidens connata* in Ontario, Crowe and Parker (1981) suggested that the Thunder Bay population, thought to be *B. connata,* may be an agamospermously-reproducing hybrid between *B. cernua* and *B. frondosa.* Both species occur in the same area and the supposed hybrid is intermediate in gross morphology between them. They further conclude that certain other taxa of *Bidens* which are poorly differentiated from *B. connata,* such as *B. eatonii,* "may likely be elements of a widespread agamic complex."

As a result of studies in the field and the examination of numerous herbarium specimens, there is good reason to question the taxonomy of *Bidens eatonii.* Whether *B. eatonii* is truly a distinct species, or whether it is a hybrid, or represents an ecotype or ecophene, remains to be seen. Clearly, additional studies are needed to resolve the taxonomic status of *Bidens eatonii* in order to determine accurately the taxonomic identity of these plants.

FLORA OF THE MERRIMACK RIVER FRESHWATER-TIDAL MARSH

The vascular flora of the Merrimack River freshwater tidal marsh consists of 88 species distributed among 66 genera in 38 families. Forty-five species are dicots and forty species are monocots. The best represented families are the Asteraceae, Cyperaceae and Poaceae.

Pteridophytes

ISOETACEAE

Isoetes echinospora Durieu Quillwort.

Occasional; at the east edge of Area 1 in the gravelly substrate in the high tide zone. *Caldwell 273, 488.*

EQUISETACEAE

Equisetum arvense L. Common Horsetail.

Occasional; throughout the marsh in the high tide zone. *Caldwell 407.*

Equisetum fluviatile L. Water Horsetail.

Common; in gravelly substrate in the high tide zone. *Caldwell 258, 426.*

Equisetum hyemale L. Scouring Rush.

Occasional; midmarsh with *Acorus calamus* at east end of study site.

Angiosperms

Dicotyledons

CABOMBACEAE

Cabomba caroliniana Gray Fanwort.

Occasional; in the Artichoke River. *Caldwell 449.*

CERATOPHYLLACEAE

Ceratophyllum demersum L. Coontail.

Occasional; in the Artichoke River. *Caldwell 448.*

RANUNCULACEAE

Caltha palustris L. Marsh-marigold.

Common; in the high tide zone throughout the marsh. *Caldwell 210.*

Ranunculus repens L. Creeping Buttercup.

Common; in gravelly areas between deep marshes in high tide zone. *Caldwell 203, 235.*

Thalictrum pubescens Pursh Tall Meadow-rue.

Common; in the backmarsh near the woods. *Caldwell 212.*

URTICACEAE

Pilea pumila (L.) Gray Clearweed.

Common; in the backmarsh near the high tide zone. *Caldwell 305, 380, 501.*

AMARANTHACEAE

Amaranthus cannabinus (L.) Sauer (= *Acnida cannabina* L.) Water-hemp.

Abundant; throughout the marsh, especially in the gravelly areas between the deep marshes. *Caldwell 244, 283, 284, 484.*

CARYOPHYLLACEAE

Sagina procumbens L. Pearlwort.

Occasional; in wet depressions in the high tide zone. *Caldwell 229.*

POLYGONACEAE

Polygonum arifolium L. Tearthumb.

Common; in the backmarsh. *Caldwell 302.*

Polygonum cuspidatum Sieb. & Zucc. Japanese Knotweed.

Common; in the backmarsh near edge of the woods. *Caldwell 268.*

Polygonum punctatum Ell. Water Smartweed.

Abundant; throughout the marsh. *Caldwell 255, 482.*

Rumex crispus L. Yellow Dock.

Common; at the edge of the marsh in the high tide zone. *Caldwell 230, 251.*

ELATINACEAE

Elatine americana (Pursh) Arn. (= *E. triandra* var. *americana* (Pursh) Fassett) Waterwort.

Abundant; growing on the mud throughout marsh. *Caldwell 291, 476, 487, 504.*

BRASSICACEAE

Cardamine pensylvanica Muhl. *ex* Willd. Pennsylvania Bitter Cress.

Occasional; at the edge of marsh, especially in gravelly areas between the deep marshes. *Caldwell 404, 423.*

PRIMULACEAE

Lysimachia ciliata L.

Occasional; at the edge of the marsh near woods. *Caldwell 468.*

Lysimachia lanceolata Walt.

Occasional; in the backmarsh. *Caldwell 248, 261.*

Lysimachia terrestris (L.) BSP. Swamp Candles.

Abundant; throughout the marsh near high tide zone. *Caldwell 454, 471.*

ROSACEAE

Potentilla norvegica L.

Uncommon; at the edge of the marsh near woods. *Caldwell 452.*

Sanguisorba canadensis L. American Burnet.

Uncommon; in open areas between the deep marshes near the high tide zone. *Caldwell 276, 511.*

FABACEAE

Amorpha fruticosa L. False Indigo.

Occasional; in the high tide zone between Area 2 and Area 3. *Caldwell 417, 520.*

LYTHRACEAE

Lythrum salicaria L. Purple Loosestrife.

Occasional; in the backmarsh. *Caldwell 239, 445.*

ONAGRACEAE

Ludwigia palustris (L.) Ell. Water-purslane.

Common; throughout the backmarsh in muddy substrate. *Caldwell 310, 381, 475.*

BALSAMINACEAE

Impatiens capensis Meerb. Spotted Touch-me-not.

Abundant; throughout the elevated areas and the backmarsh. *Caldwell 306.*

APIACEAE

Cicuta bulbifera L. Bulb-bearing Water-hemlock.

Occasional; in the backmarsh in Area 1. *Caldwell 345, 522.*

Cicuta maculata L. Water-hemlock.
Common; in the backmarsh. *Caldwell 451, 436.*
Sium suave Walt. Water-parsnip.
Abundant; throughout the marsh, especially in the stony areas between the deep marshes. *Caldwell 240, 322, 474.*

APOCYNACEAE
Apocynum cannabinum L. Indian-hemp.
Occasional; in the high tide zone between Area 2 and Area 3. *Caldwell 440, 505.*

LAMIACEAE
Lycopus americanus Muhl. Water-horehound.
Common; in the backmarsh. *Caldwell 242, 323, 379, 495.*
Mentha arvensis L. Water Mint.
Common; throughout the marsh in the high tide zone. *Caldwell 242, 462.*
Physostegia leptophylla Small (= *P. arboriginorum* Fern.)
Occasional; in the shade near the high tide zone between Area 2 and Area 3. *Caldwell 512.*
Scutellaria lateriflora L. Skullcap.
Occasional; in the backmarsh near the edge of the woods. *Caldwell 378, 499.*

CALLITRICHACEAE
Callitriche verna L. (= *C. palustris* L.) Water-starwort.
Occasional; along the edge of the Indian River and the west side of the island near the Artichoke River. *Caldwell 228, 432.*

SCROPHULARIACEAE
Chelone glabra L. Turtlehead.
Common; in the backmarsh and the edge of the island near the Artichoke River. *Caldwell 329, 336, 509.*
Lindernia dubia (L.) Pennell False Pimpernel.
Common; in the high tide zone at the edges of the deep marshes. *Caldwell 262, 480.*
Mimulus ringens L. Square-stem Monkey-flower.
Common; throughout the marsh in the high tide zone. *Caldwell 245, 441, 469, 521.*

RUBIACEAE

Galium palustre L. Bedstraw.

Occasional; in the muddy areas of the backmarsh in the high tide zone. *Caldwell 217, 224, 500.*

ASTERACEAE

Aster novi-belgii L. New York Aster.

Abundant; throughout the marsh in the high tide zone at the edge of the woods. *Caldwell 338, 516, 519.*

Bidens cernua L. Beggar's-ticks.

Abundant; throughout the midmarsh but more frequently in the backmarsh. *Caldwell 281, 303, 309, 328, 481.*

Bidens connata Muhl. *ex* Willd.

Common; throughout the marsh. *Caldwell 355, 358.*

Bidens eatonii Fern.

Common; in the gravelly and elevated areas of the marsh. *Caldwell 506, 507, 510, 525.*

Bidens frondosa L.

Occasional; in the backmarsh in the high tide zone. *Caldwell 335, 340, 524.*

Eupatorium dubium Willd. *ex* Poir. Joe-pye Weed.

Common; at the edge of the marsh in the high tide zone. *Caldwell 274, 496.*

Eupatorium perfoliatum L. Boneset.

Abundant; in the elevated areas and the backmarsh in the high tide zone. *Caldwell 437, 465, 497.*

Solidago sempervirens L. Seaside Goldenrod.

Common; between the deep marshes in the high tide zone. *Caldwell 325, 517, 518.*

Tussilago farfara L. Coltsfoot.

Uncommon; between Area 2 and Area 3 in the high tide zone. *Caldwell 405.*

Monocotyledons

ALISMATACEAE

Alisma subcordatum Raf. (= *A. plantago-aquatica* var. *parviflorum* (Pursh) Torr.) Water-plantain.

Uncommon; in the backmarsh of Area 1. *Caldwell 271, 478.*

Alisma triviale Pursh (= *A. plantago-aquatica* var. *americana* Schultes & Schultes) Water-plantain.
Uncommon; in the backmarsh of Area 3. *Caldwell 494.*

Sagittaria graminea Michx. var. *graminea* (*S. eatoni* J. G. Sm.)
Abundant; throughout the marsh in muddy silty substrate. Occurring as sterile rosettes in the low tide zone. *Caldwell 232, 241, 254, 261, 279, 280, 429, 439.*

Sagittaria latifolia Willd. Arrowhead.
Abundant; throughout the middle and backmarsh in muddy substrate. *Caldwell 264, 278, 331, 332, 477, 493.*

HYDROCHARITACEAE

Elodea nuttallii (Planch.) St. John Waterweed.
Abundant; throughout the marsh in muddy substrate or in large patches in open areas in the low tide zone. *Caldwell 222, 257, 294, 433.*

Vallisneria americana Michx. Tape-grass.
Common; washed up on shore throughout the marsh. *Caldwell 277, 498.*

POTAMOGETONACEAE

Potamogeton crispus L. Curly-leaved Pondweed.
Occasional; rooted in the mud in the low tide zone or washed up on shore. *Caldwell 221, 479.*

Potamogeton nodosus Poir.
Occasional; in the muddy substrate of the high tide zone; plants vegetative only. *Caldwell 218, 333, 412, 527.*

Potamogeton perfoliatus L. Clasping-leaved Pondweed.
Occasional; rooted in the mud in the low tide zone and at the edges of the Artichoke River. *Caldwell 219, 420, 450.*

Potamogeton robbinsii Oakes Robbins' Pondweed.
Uncommon; in the Artichoke River. *Caldwell 447.*

ARACEAE

Acorus calamus L. Sweet-flag.
Abundant; occurs as a large zone mid-marsh with scattered populations near the edges. *Caldwell 204, 402, 411.*

Peltandra virginica (L.) Schott & Endl. Arrow-arum.
Common; in the deep mud of backmarsh. *Caldwell 424, 434.*

LEMNACEAE

Wolffia columbiana Karst. Water-meal.

Uncommon; washed up on shore. *Caldwell 313.*

COMMELINACEAE

Commelina communis L. Asiatic Dayflower.

Occasional; in the high tide zone between Area 2 and Area 3. *Caldwell 459.*

ERIOCAULACEAE

Eriocaulon parkeri Robins. Pipewort.

Occasional; at the east edge of Area 1 in gravelly substrate in the high tide zone. *Caldwell 259, 272, 319, 492.*

JUNCACEAE

Juncus acuminatus Michx.

Occasional; in the gravelly substrate between the deep marshes. *Caldwell 234, 253, 446, 455.*

CYPERACEAE

Carex hormathodes Fern.

Uncommon; in the high tide zone at the east edge of Area 1. *Caldwell 427.*

Carex paleacea Wahlenb.

Occasional; in the gravelly substrate between the deep marshes and elevated backmarsh. *Caldwell 205, 413.*

Carex stipata Muhl. *ex* Willd.

Uncommon; in the high tide zone at east edge of Area 1. *Caldwell 421.*

Cyperus bipartitus Torr. (= *C. rivularis* Kunth)

Occasional; in the gravelly substrate in the high tide zone. *Caldwell 491.*

Cyperus esculentus L. Yellow Nut-grass.

Occasional; in the gravelly substrate in the open areas. *Caldwell 292.*

Dulichium arundinaceum (L.) Britt. Three-way Sedge.

Frequent; in large clumps in the gravelly areas and in the backmarsh. *Caldwell 456, 508.*

Eleocharis smallii Britt. Spike Rush.

Frequent; in the gravelly areas and the elevated borders of the islands. *Caldwell 211, 247, 287, 408, 425, 457.*

Scirpus fluviatilis (Torr.) Gray River Bulrush.
Frequent; in the midmarsh and elevated borders, particularly around the islands. *Caldwell 285, 312, 400, 401, 430, 443, 503.*

Scirpus pungens Vahl. (*S. americanus* of American authors, misapplied to this taxon) Three-square Bulrush.
Abundant; throughout the marsh in the low tide zone and the gravelly areas. *Caldwell 214, 233, 249, 270, 286, 442.*

Scirpus smithii Gray
Uncommon; in the gravelly substrate with *Eriocaulon parkeri* at the east end of Area 1 near the high tide zone. *Caldwell 490.*

Scirpus tabernaemontanii K. C. Gmel. (= *S. validus* Vahl.) Great Soft-stem Bulrush.
Abundant; midmarsh in the silty muddy substrate. *Caldwell 213, 256, 431.*

POACEAE

Agrostis stolonifera L. var. *stolonifera* (= *A. stolonifera* var. *major* (Gaud.) Farw.; *A. alba* var. *stolonifera* (L.) Sm.) Redtop.
Occasional; at the edge of the marsh in the high tide zone. *Caldwell 470.*

Calamagrostis canadensis (Michx.) Beauv. Bluejoint.
Frequent; at the edge of the marsh in the high tide zone. *Caldwell 227, 428.*

Dactylis glomerata L. Orchard Grass.
Uncommon; at the edge of marsh in the high tide zone near the woods. *Caldwell 206.*

Panicum dichotomiflorum Michx. var. *geniculatum* (Wood.) Fern.
Uncommon; in a gravelly area of the river bank that was cleared by landowner. *Caldwell 344.*

Phalaris arundinacea L. Reed Canary Grass.
Occasional; in the high tide zone throughout the marsh. *Caldwell 208, 414.*

Spartina alterniflora Loisel. Saltwater Cord Grass.
Frequent; in large clumps in the silty substrate near the low tide zone. *Caldwell 485, 506.*

Spartina pectinata Link Freshwater Cord Grass.
Frequent; in the gravelly substrate in the high tide zone. *Caldwell 236, 250, 444.*

Zizania aquatica L. var. *aquatica* Southern Wild-rice.
Abundant; scattered throughout the marsh, but especially abundant in the deep mud of the backmarsh. *Caldwell 260, 267, 486.*

SPARGANIACEAE

Sparganium eurycarpum Engelm. Large-fruited Bur-reed.
Occasional; in the backmarsh and bordering the Indian River. *Caldwell 269, 304, 418.*

TYPHACEAE

Typha angustifolia L. Narrowleaf Cattail.
Occasional; in the elevated areas bordering the island near the Indian River. *Caldwell 223.*

PONTEDERIACEAE

Pontederia cordata L. Pickerel-weed.
Abundant; in the deep mud of the backmarsh and occasionally the midmarsh. *Caldwell 238, 467.*

IRIDACEAE

Iris pseudacorus L. Yellow Iris.
Occasional; in the high tide zone and the elevated areas bordering the islands. *Caldwell 201, 226.*

Iris versicolor L. Blue Flag.
Occasional; in the high tide zone between the deep marshes. *Caldwell 202.*

CONCLUSION

Several biotic and abiotic factors influence the composition and distribution of vegetation in a freshwater tidal marsh. Three environmental parameters that may be related to plant community structure were explored, including salinity, organic content of the soil, and water level fluctuation.

Although salinity is a hydrological component of a freshwater tidal marsh, levels of less than 5‰ measured at the study site were probably too low to be a major influence on the structure of plant cover types. Also, the fact that salinity occurred near the

end of the growing season seemed to further negate its influence on community structure.

Soil organic content measurements indicate that a large percentage of the marsh, encompassing many cover types, contains mineral soil with a low level of organic matter. Although species diversity is the highest in backmarsh cover types where soil organic content is highest, more sampling needs to be done to substantiate any conclusions.

On the other hand, duration of inundation at the plant/soil interface appears to be an important factor in structuring marsh cover types. Species diversity is lowest in cover types such as those dominated by *Spartina alterniflora* and *Scirpus pungens,* where duration of flooding is the longest (16 hr./day). Few emergent species can tolerate this extensive period of inundation. Mid- to backmarsh cover types such as those dominated by *Acorus calamus* and *Zizania aquatica* have more diversity. However, this analysis does not hold true for rocky shore areas where presumably the high degree of disturbance is an overriding influence on vegetation patterns.

Two other important factors contributing to plant community structure in the Merrimack River marsh that should be mentioned here are plant growth forms and physical disturbance by ice floes. The most successful plants in this fluctuating environment are either annuals or strongly rhizomatous perennials. A proliferation of rhizomes allows these plants to take hold in areas of constant sediment deposition and erosion, while storing nutrients for early emergence and rapid growth. The seeds of annuals, in contrast, find protection in the microrelief of the marsh surface and rocky shoreline.

The Merrimack River is a relatively large and rapidly moving river that partially freezes during the winter. Therefore, ice floes also have a major impact on the vegetation of the marsh and rocky shoreline. Plants along the banks are sheared by ice scouring. Additionally, sediments containing seeds and rhizomes are entrapped and transported by ice chunks drifting up and downstream on tidal and river currents, often being deposited along the river's edge or carried out to sea.

Freshwater tidal marshes are the least studied wetlands in the U.S. (Odum et al., 1984). This environment is dynamic, with many distinctive plant species. Research in many more freshwater tidal rivers is surely needed to better understand this unique habitat.

ACKNOWLEDGMENTS

We thank A. Linn Bogle, T. Lee and A. Mathieson for their helpful comments on the manuscript. This research was funded in part by the the Massachusetts Natural Heritage and Endangered Species Program and the University of New Hampshire Central University Research Fund (#3012).

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DEPARTMENT OF PLANT BIOLOGY
UNIVERSITY OF NEW HAMPSHIRE
DURHAM, NH 03824

RHODORA, Vol. 94, No. 877, pp. 98–99, 1992

NEW ENGLAND NOTE

AN INDIGENOUS POPULATION OF *CLINTONIA BOREALIS* (LILIACEAE) ON CAPE COD

SHIRLEY G. CROSS

On August 29, 1990 in East Sandwich, MA I was collecting botanical specimens for the Green Briar Nature Center of the Thornton W. Burgess Society, and was startled to come upon a colony of approximately 50 plants of *Clintonia borealis* (Ait.) Raf. The colony was growing on a wooded bank above a swampy area traversed by spring-fed streams running down into the adjoining saltmarsh. Only a few plants appeared to have flowered. There were no fruiting scapes.

I returned to the site in early May of 1991. Three budded scapes were present. On this occasion an additional colony was discovered which had no flowering scapes, possibly due to the close shading of *Smilax rotundifolia* L.

The entire area, swamp and banks, is in the category described by Svenson and Pyle (1979) under the heading of "The fresh borders of saltmarshes." It has the black soil they speak of and the rich flora of *Symplocarpus foetidus* (L.) Nutt., *Dryopteris simulata* Davenp., *Woodwardia areolata* (L.) Moore, *Arisaema triphyllum* (L.) Schott, *Viola cucullata* Ait., and *Chrysosplenium americanum* Schwein. overshadowed by old red maples (*Acer rubrum* L.), tupelo (*Nyssa sylvatica* Marsh.), beech (*Fagus grandifolia* Ehrh.) and witch hazel (*Hamamelis virginiana* L.).

I enlisted the help of Dr. Walter H. Hodge and returned to the site with him on May 14th, 1991. On seeing the site he agreed with me in thinking it to be an old undisturbed area. He photographed the Clintonia colony and the blossoming scape. I afterwards pressed the scape and basal leaves and am depositing the specimen with copies of the photographs in NEBC, under the Green Briar Nature Center's label. (The Green Briar Nature Center is the teaching arm of the Thorton W. Burgess Society.)

Copies of the photographs are also deposited at SPWH and at the Herbarium of the Cape Cod Museum of Natural History in Brewster, Massachusetts.

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THORTON W. BURGESS SOCIETY
6 DISCOVERY HILL ROAD
E. SANDWICH, MA 02537

NEBC AND NEW ENGLAND WILDFLOWER SOCIETY SYMPOSIUM SCIENTIFIC AND MANAGEMENT ISSUES IN RARE PLANT CONSERVATION

The New England Botanical Club and the New England Wildflower Society will sponsor a symposium on the scientific and management issues in rare plant conservation. Symposium topics will include taxonomic issues in plant conservation, setting priorities for protection, re-introduction and transplantation, and habitat management. The symposium will be held on March 21, 1992 at Bentley College in Waltham, Massachusetts. Additional details and registration materials will be mailed in January, 1992. For information, write to:

Symposium Committee
The New England Botanical Club
Harvard University Herbaria
22 Divinity Avenue
Cambridge, MA 02138

RHODORA, Vol. 94, No. 877, pp. 100–101, 1992

BOOK REVIEW

Alice F. Tryon and Bernard Lugardon. 1991. *Spores of the Pteridophyta: Surface, Wall Structure, and Diversity Based on Electron Microscope Studies.* 648 pp. Springer-Verlag, 175 Fifth Ave, New York, NY 10010. ISBN 0-387-97218-8. (Price: $98.00, hardcover.)

The spore-wall features of spore-dispersed plants such as ferns and clubmosses have long been known for their beauty and variation. In a new book by Alice Tryon and Bernard Lugardon, these features have been exhaustively portrayed in an unparalleled compendium of data on spore-wall ultrastructure. This abundantly illustrated volume focuses both on surface features as seen under the scanning electron microscope and the interior-wall features visible in transmission electron micrographs. It will prove a landmark volume for students of plant evolution and ecology as well as sedimentary petrologists and commercial groups interested in identifying productive sedimentary strata.

This work is the product of a remarkable international cooperation; Bernard Lugardon developed the transmission electron micrography in France and Alice Tryon pursued the scanning electron microscope work in the United States. Their years of work together have paid off in a highly integrated volume with a single message supported by two enormous data sets relevant to the same biological issue, the significance of spore design to systematics and evolutionary studies in the spore-dispersed plants.

The book includes two sections, a general introduction and a survey of the genera. The introduction provides a valuable overview of spore structure and development; it is rich in detail and at the same time accessible. The long-standing confusion about the chemical and structural correspondence of seed-plant and fern spore coats is resolved in a lucid and well-illustrated essay: we can now say that there is little if any homology between the two wall structures. At the same time we gain an understanding of the deposition process resulting in the complex, attractive structure of the mature spore.

The heart of the book is the profusely illustrated survey of genera. Worldwide in scope, the survey includes a broad representation of all the major groups of ferns, lycopsids, horsetails, and psilophytes. The text for each genus addresses the circum-

scription and size of the genus, its range, and details of spore size and morphology, as well as a longer section outlining the relationships of the group based on spore morphology and insights into variation within the group. A literature summary ends each generic treatment. The illustrations for each genus include an array of Scanning Electron Microscope images of the surface features of the spores, and Transmission Electron Micrographs of interior features are often included as well. The images are technically of the highest quality, and the standard magnification for all whole-spore images allows easy visual comparison of spore size. The utility of the volume is further increased with a glossary of the technical terms relevant to characterizing spore morphology.

This work of Tryon and Lugardon is a milestone in the understanding of spore wall structure and development. The exhaustive review of spore diversity coupled with the well developed analytic section in the introduction supports the continued development of spore architecture as a character system for systematic studies in the ferns and other spore-dispersed plants.

DAVID S. BARRINGTON
PRINGLE HERBARIUM
DEPARTMENT OF BOTANY
UNIVERSITY OF VERMONT
BURLINGTON, VT 05405-0086

RHODORA, Vol. 94, No. 877, p. 102, 1992

BOOK REVIEW

Day, Robin and Paul M. Catling 1991. *The Rare Plants of Prince Edward Island.* Syllogeus Series No. 67. Canadian Museum of Nature. Prepaid orders available from the Canadian Museum of Nature, Direct Mail Section, P.O. Box 3343, Station D., Ottawa, Ontario, Canada K1P 6P4. (Price: $4.95.)

This booklet is a continuation of the rare plants of Canada series. It lists the rare vascular plants of Prince Edward island and includes a range map in Prince Edward Island with generalized locations, references, the ranges in North America, habitat, and status in other provinces.

The rare vascular plants of Prince Edward Island is a must for the person interested in the rare species of Canada and North America. The style is similar to those published for the other provinces. The only plant listed that probably does not belong is *Phragmites australis,* an introduced weedy species throughout North America.

C. BARRE HELLQUIST
DEPARTMENT OF BIOLOGY
NORTH ADAMS STATE COLLEGE
NORTH ADAMS, MA 01247

RHODORA, Vol. 94, No. 877, pp. 103–105, 1992

BOOK REVIEW

A. Borhidi. 1991. *Phytogeography and Vegetation Ecology of Cuba.* 858 pp. (including 380 figs. as photographs, graphs, maps, diagrams, plus 16 colored plates, and a packet with "Map of the Natural Potential Vegetation of Cuba," in color, 1:1,250,000). Akadémiai Kiadó (publishing house of the Hungarian Academy of Sciences), Prielle Kornélia u. 19-35, H-1117 Budapest, Hungary. ISBN 963 05 5292 7. (Price: $74, cloth.)

Phytosociological studies and classification of the vegetation of European countries are well known. The school producing such studies in North America has been small and is represented most recently by Pierre Dansereau (1957). In the Caribbean area, Stehlé published such treatments for Guadeloupe (Stehlé, 1935), as did Ciferri for Hispaniola (Ciferri, 1936) and Dansereau for Puerto Rico (Dansereau, 1966). In this volume Borhidi applies such techniques to the vegetation of Cuba.

Following the"victory of the Popular Revolution" in Cuba in 1959, botanical research was re-established in the sixties with extensive programs to recollect the vegetation for a new *Flora of the Republic of Cuba* (Capote, 1988). Along with the building of collections, special studies had as preliminary tasks: "typification of the vegetation units; analysis of the structure and composition of the vegetation units; comprehensive bioclimatological studies of whole country; exploration of the inner and outer phytogeographic relationships in Cuba in order to prepare a new 'phytogeographic regionalization' of Cuba to link all in geobotanic work which has been prepared for most countries in Europe but which is available only in a few tropical countries" (Borhidi, 1991). The author of this book is A. Borhidi of Hungary, the principal contributor to these studies, but the work also includes the studies of H. Manitz and J. Bisse of the German Democratic Republic, V. Samek of Czechoslovakia, and many Cuban botanists who were their students and protegés.

Borhidi's volume contains a most welcome concise study of the geography of Cuba with a map showing current divisional boundaries. There is a chapter devoted to updating our knowledge of the various relationships between soil and vegetation, which historically have been important to Cuba. Borhidi also analyzes

the vegetation on the basis of life-forms and offers a phytogeographic characterization of the flora of Cuba, on which a vegetational map is based. A life-form analysis is given for the 6375 species of spermatophytes to be included in the new *Flora of the Republic of Cuba*. Woody plants comprise 53.3% of these species; 40 different woody formations are recognized by Borhidi. These formations are comparable to the descriptive units given by Capote et al. (1988), but are described here with pseudo-Latin phrase names, which even the author occasionally does not repeat correctly. The map of the natural potential vegetation by Borhidi and Muñiz is at the scale of 1:1,250,000, dated 1969–1970 (in this 1991 volume), and is approximately 12″ by 36″. Thirty-three vegetational units are given in six basic colors, some also overlaid with lines and dots. Three of the colors are intended to be subdivided, but the divisions are not readily distinguishable in my copy.

Over half of the book is devoted to a systematic survey of the plant communities which are classified in a phytosociological hierarchy of 27 classes, 55 orders, 86 alliances, and 186 associations. Each is named, again with a pseudo-Latin epithet, dated and described, with an author's name cited. The implication of priority is indicated in abbreviations such as *nom. nud.*, *nova, hoc locus, syn.*, or *ined.* Some comparable categories are recognized by Ciferri or Stehlé, but are renamed or emended in this volume. A long appendix, as an out-of-place Table 25, lists the taxa found in relevés in the 40 communities of woody plants. Both life-forms and geographic elements are indicated. Taxa are listed alphabetically. There is an index to subject matter, including figure and table references, and an index to Latin plant names as used outside of the phytosociological tables.

A good bibliography is given which shows how much of the available literature on Cuba has unfortunately not reached our local libraries.

A personal visit to Cuba is not possible for most botanists at the present time. However, an understanding of the complexities of the vegetational units in the flora of Cuba is easily obtained from this comprehensive work by Dr. Borhidi, who makes clear his contention that ecological research should be geobotanical, chorographical, and plant geographical. The anticipated *Flora of the Republic of Cuba* will be a welcome companion volume to this study.

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RICHARD A. HOWARD
HARVARD UNIVERSITY HERBARIA
CAMBRIDGE, MA 02138

NEBC AWARD
FOR THE SUPPORT OF BOTANICAL RESEARCH

The New England Botanical Club will again offer an award of $1000 in support of botanical research to be conducted in relation to the New England Flora during 1992. This award is made to stimulate and encourage botanical research on plant species or communities which occur in New England, and to make possible visits to the New England region by those who would not otherwise be able to do so. The award will be given to the graduate student submitting the best research proposal, and is not limited to graduate students at New England institutions nor to members of the New England Botanical Club. Preference will be given to research dealing with field studies in systematic botany, biosystematics, plant ecology, or plant conservation biology. Applicants should submit a proposal of no more than three double-spaced pages, a budget (the budget will not affect the amount of the award), and a curriculum vitae. Two letters, one from the student's major professor, in support of the proposed research are also required. Proposals and supporting letters should be sent before 28 February to:

Awards Committee
The New England Botanical Club
22 Divinity Ave
Cambridge, MA 02138

MEETING ANNOUNCEMENT AND CALL FOR ABSTRACTS NEW ENGLAND BOTANY GRADUATE STUDENTS

The seventh New England Botany Graduate Student Meeting will be hosted by the Department of Plant Biology at the University of New Hampshire, Durham, NH on Saturday April 11, 1992. Attendance is open to all. Paper presentations will be largely restricted to graduate student research (completed or in progress) representing all areas of botany (systematics, ecology, reproductive biology, anatomy, physiology, etc.). Time slots for paper presentations are limited and prior registration is required. Abstracts are due by Monday, March 13, 1992.

For information and abstract forms, contact:

Linda Fahey or Lenny Lord
Department of Plant Biology
University of New Hampshire
Durham, NH 03824
Tel.:(603) 862-3860

RONALD L. STUCKEY INITIATES ENDOWMENT FUND FOR THE OHIO STATE UNIVERSITY HERBARIUM

Ronald L. Stuckey, Professor of Botany at The Ohio State University, recently presented a gift of $30,000 to the University's Foundation to initiate an endowment for the support of the University Herbarium. The presentation was made as a final surprise announcement at Professor Stuckey's retirement party celebrating his 26 years of teaching at the University.

Designated as the Ronald L. Stuckey Herbarium Fund, the endowment will aid in the studies of the flora of Ohio, a particular concern of the donor. The establishment of the endowment fund for the University Herbarium not only marks the occasion of Dr. Stuckey's retirement from teaching, but also commemorates the 100th anniversary of The Ohio State University Herbarium, which was founded in 1891 by the University's first Professor of botany, Dr. William A. Kellerman. Professor Stuckey served as curator of the herbarium from 1967 through 1976.

THE 1991 JESSE M. GREENMAN AWARD

The 1991 Jesse M. Greenman Award has been won by Scott Zona for his publication "A monograph of *Sabal* (Arecaceae: Coryphoideae)," published in *Aliso* 12: 583–666, 1990. This monographic study is part of a Ph.D. dissertation from Claremont Graduate School, Claremont, California, under the direction of Dr. Sherwin Carlquist.

The Greenman Award, a certificate and a cash prize of $500, is presented each year by the Missouri Botanical Garden. It recognizes the paper judged best in vascular plant or bryophyte systematics based on a doctoral dissertation published during the previous year. Papers published during 1991 are now being accepted for the 24th annual award, which will be presented in the summer of 1992. Reprints of such papers should be sent to:

Dr. P. Mick Richardson
Greenman Award Committee
Missouri Botanical Garden
P.O. Box 299
St. Louis, MO 63166-0299, U.S.A.

In order to be considered for the 1992 award, reprints must be received by June 1, 1992.

THE NEW ENGLAND BOTANICAL CLUB
22 Divinity Avenue
Cambridge, MA 02138

The New England Botanical Club is a non-profit organization that promotes the study of plants of North America, especially the flora of New England and adjacent areas. The Club holds regular meetings, has a large herbarium of New England plants, and a library. It publishes a quarterly journal, RHODORA, which is now in its 94th year and contains about 400 pages a volume.

Membership is open to all persons interested in systematics and field botany. Annual dues are $35.00, including a subscription to RHODORA. Members living within about 200 miles of Boston receive notices of the Club meetings.

To join, please fill out this membership application and send with enclosed dues to the above address.

Regular Member	$35.00
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For this calendar year	_____
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Vol. 93, No. 876, including pages 307–412, was issued November 14, 1991.

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RHODORA

JOURNAL OF THE NEW ENGLAND BOTANICAL CLUB

Vol. 94 April 1992 No. 878

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Cover Illustration

Rhexia virginica L., meadow beauty, is found from Nova Scotia to Georgia, but is rare at the northern limits of its range. The only northern outlier of the tropical family Melastomataceae, it has distinctive 3-veined leaves and geniculate stamens. Original artwork by Josephine Ewing.

Rhodora

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FLORAL VARIATION AND TAXONOMY OF *LIMNOBIUM* L. C. RICHARD (HYDROCHARITACEAE)

RICHARD M. LOWDEN

ABSTRACT

Floral and geographic evidence for infraspecific classification of the monotypic genus *Limnobium* (incl. *Hydromystria*) native to the Americas are presented. A continuum in floral form and a conspicuous overlap in patterns of flower variation between populations disclose the presence of just one latitudinally diverging species, *Limnobium spongia* (Bosc) Steudel, in which two subspecies, *L. spongia* subsp. *spongia* and *L. spongia* subsp. *laevigatum* (Humb. & Bonpl. ex Willd.) Lowden, *comb. nov.*, are recognized. Numerical analysis of floral variation in living populations and their evolutionary trends are treated for these two subspecies. Special field collections of this freshwater, non-submerged, monoecious plant were made throughout the known range of the genus in eastern United States, West Indies and South America. Population samples allowed critical morphological observations on male and female flowers, for which consistent and continuous variation was found in the form and number of petals, stamens, staminoides, stigmas, carpels and locules.

Key Words: *Limnobium,* monospecific, *Limnobium spongia* subspecies, infraspecific variation, flower variation, population diversity, aquatic plant, Americas

INTRODUCTION

The first documented field observations of floral variation in a population of this New World native aquatic plant were made by José Celestino Mutis, director of the Royal Botanical Expedition of the New Kingdom of Granada at Santa Fe de Bogotá (Bogotá), Colombia. On two occasions (April 29, 1783 and January 26, 1784) he wrote in his diary (Instituto Colombiano de Cultura

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Hispanica, 1958) concerning the problems encountered to draw and classify the inconsistencies found in flowers of this interesting plant which grew then, and still abounds today, in lagoons and stagnant water about Bogotá.

Beyond his interest to conserve flowering material for drawing purposes, Mutis had collected a flower sample that enabled him to determine some of the variations that characterize the unisexual flowers of this plant for this particular locality in south America. In male flowers, Mutis found three sepals, three petals, and usually seven stamens but sometimes nine ["Por lo regular hallé siete machos y pocos de nueve. . . . casi invisibles."]. At the Madrid Botanical Garden (Spain), Mutis Plates 259, 260 & 260A (Díaz-Piedrahita, 1985, Laminas XXXV–XXXVII) show male flowers with conspicuous bilobed petals and seven stamens. Even though Mutis did not refer in his diary to these petals as being bilobed, these plates are proof that they were observed as such over two centuries ago. It is somewhat surprising to note that this obvious character has been overlooked in the herbarium and in nature until now. In the same manner, Mutis found considerable variation in female flowers ["Muchos pistilos con inconstancia"], having three sepals, apparently no petals, nine to 15 stigmatic lobes (Plate 260; shows a flower with 11 stigmatic lobes), ovary uniloculed, and fruit elongate (Plates 260 and 260A). A keen sense of observation in the field led Mutis to consider he did not have at hand ordinary flowers with a constant number of parts, but instead a highly variable plant whose classification would require further field observations.

Two decades later, flower variants of a similar plant population were observed by M. Bosc (1807) and L. C. Richard (1814; described as *Limnobium*) from a marsh in South Carolina (Basse-Caroline), United States. The male flowers were described as having three sepals, three petals, eight to 12 stamens, sometimes more [Bosc, 1807: "huit a douze étamines, et quelquefois plus, ..."] and two or three staminodes [Richard, 1814: "La colonne staminifère est terminée à son sommet par deux ou trois petits filamens tres-courts et aizus."; Planche no. 8 (B-7) shows nine stamens and at least one staminode]. Female flowers demonstrated three sepals, three petals, three staminodes [Planche (E-2) shows two of these staminodes], 12 stigmatic lobes [Bosc, 1807; ". . . six styles profundément bifurqués . . ."], ovary six loculed, fruit glo-

bose. Richard (1814) was not surprised to find male flowers with different numbers of stamens considering the number of parts found in other members of the Hydrocharitaceae.

It is only in recent years during the present decade that comparable knowledge of another population has been presented by Armando T. Hunziker (1982) from Cabalango (Dept. Punilla), Province of Córdoba, Argentina. In male flowers he counted three sepals, three petals, six stamens only and no staminodes; while, in female flowers there were three sepals, zero to three petals (sometimes one or two, rarely three), four or five staminodes (usually five in pairs or solitary opposite the sepals 2+2+1, if four, then 2+1+1 or 2+2), stigmas usually six but sometimes five (ten or 12 stigmatic lobes), ovary uniloculed with four or five inconspicuous placental partitions, and fruits oblong to ovoid. Despite his proposal to maintain the Middle and South American plant as a distinct genus (*Hydromystria*), Hunziker rightfully considered our present knowledge of this plant to be incomplete, hence a better classification depends on new data.

As such, up until now, these exact but only too few isolated field observations explain neither the extent nor the frequency of flower variants in populations that would permit the taxonomic treatment of this plant throughout its known geographic distribution in the Americas. In like manner, the same applies to herbarium studies (Díaz-Miranda et al., 1981; Cook and Urmi-König, 1983) that make assertations concerning classification of this plant based on the meager existence of dried specimens, whose exact identity based on the number of flower parts is for the most part unknown. These treatments have not recognized the occurrence of flower variants in living populations nor on dried herbarium material. Consequently, due to insufficient field studies, not only the taxonomy but the developmental biology has been misinterpreted for this plant.

At different geographical locations in the Americas, I have collected and observed the extent of variation in unisexual flowers along with their frequency of expression. The population at each locality was recognized as a dynamic and natural unit demonstrating observable biogenetic tendencies which relate to the number and kind of flower structures found in flower variants. Based on these new findings, I present a corresponding infraspecific classification.

Table 1. Traits characterizing subspecies of *Limnobium spongia*.

Character	Primitive: *L. spongia* subsp. *spongia*	Derived: *L. spongia* subsp. *laevigatum*
Male:		
Petals	essentially unlobed	1–2 and more lobes
Stamens and staminodes	many (form 3–4 trimerous whorls)	few (form 1–3 trimerous whorls)
Female:		
Petals	3 conspicuous, essentially unlobed	apetaly common *or* petals less than 3, with 1–2 and more lobes
Staminodes	more numerous	fewer
Stigmas	many deeply-bifid (fill 2nd and 3rd trimerous stylar whorls)	fewer, somewhat less-bifid (fill 1st and 2nd trimerous stylar whorls)
Carpels	almost closed, globose ovary with 6–9 parietal placental divisions (pseudolocules, Fig. 3f–g)	open, elliptic ovary one loculed with 3–6 intruding parietal placentae (Fig. 2f–g)

SUBSPECIES CHARACTERIZED: PRIMITIVE VERSUS DERIVED TRAITS

Critical observations of floral structures disclose a consistent and continuous integration in the number and form of stamens, stigmas, staminodes, petals, locules and carpels that negates the existence in the Americas of two distinct monotypic genera, *Hydromystria* and *Limnobium* (Ascherson and Gürke, 1889; Rydberg, 1909; Díaz-Miranda et al., 1981; Hunziker, 1982), and of even the single genus *Limnobium* having two or more species (Dandy, 1959; Cook et al., 1974; Cook, 1982; Cook and Urmi-König, 1983). These new field results based on knowledge of living populations elucidate a single genus with just one very dynamic species, *Limnobium spongia* (Bosc) Steudel, for which a subspecies distinction was determined based on the inseparable nature of two diverging developmental patterns that demonstrate latitudinally phylogenetic trends for the establishment of primitive and derived floral traits. These traits which characterize the two recognized subspecies of *Limnobium spongia* are summarized in Table 1.

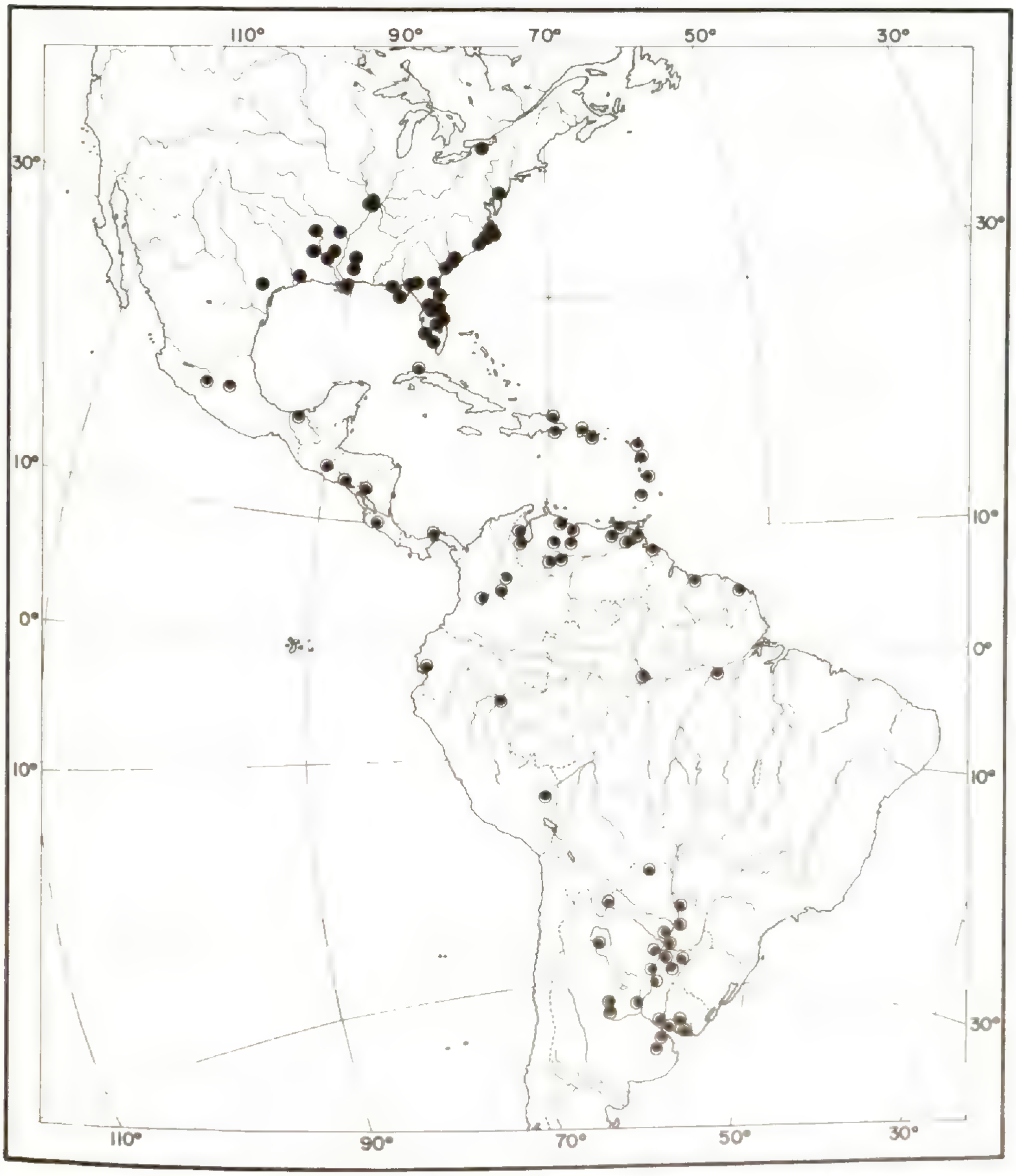

Figure 1. Distribution of the monotypic genus *Limnobium* in the Americas, showing *L. spongia* subsp. *spongia* (●) in the United States and *L. spongia* subsp. *laevigatum* (◐) in the West Indies (Greater and Lesser Antilles), Mesoamerica and South America.

Throughout its known geographic distribution in the Americas (Figure 1), *Limnobium spongia* is a species of great vegetative and reproductive plasticity. Its transitional nature is reflected by the terrestrial to aquatic habitats it occupies and by its variable imperfect floral states, which demonstrate a latitudinal continuum in specialization from one subspecies to the other.

Limnobium spongia subsp. *spongia* is more northern in latitude (limited to the eastern United States, Figure 1). In its northern-

Figure 2. Staminate and pistillate plants of *Limnobium spongia* subsp. *laevigatum* from the Dominican Republic (*Lowden 3601*): **a.** floating male plant segment with fleshy aerenchymous leaf blades and completely extended staminate pedicel; **b.** ventral view of male flower having 3 sepals, 3 petals and 6 fertile stamens; **c.** single longitudinally dehiscing mucronate-tipped stamen; **d.** female

most range (Horseshoe Lake, Illinois), this subspecies appears to have a greater number of floral parts with fewer structural modifications. Plants are generally larger, having expanded leaf blades with prominent nerves. In both male and female flowers, three unlobed petals is a relatively constant trait.

On the other hand, *Limnobium spongia* subsp. *laevigatum* occurs in more southern latitudes (south of the United States, Figure 1). Here more specialization takes place in latitudes further south (from the Dominican Republic to Argentina), where there is evidence of greater reductions in the number of floral parts. Plants are usually smaller and leaves inconspicuously nerved. More bilobed and irregularly-lobed petals are found in flowers of both sexes of this subspecies. In female flowers, apetaly and connation between concordant stigmatic lobes are considered to be highly specialized conditions, just as is reduction in fused carpel walls of fruits.

FLORAL STRUCTURES: UNISEXUAL FLOWERS

This comparative study of the gross floral morphology treats flowers collected at anthesis, which occurs between noon and late afternoon before the sun loses its thermal intensity. At this time of day in all populations, flower stalks are completely extended and a spectacular array of both male and female flowers can be observed above the water surface. Plants collected otherwise might be partly responsible for the misconception that plants are "rare" or "uncommon," stamens are "sessile" (Hauman, 1915; Hunziker, 1981), male flowers are "less common" and female inflorescences are "much more commoner" (Cook and Urmi-König, 1983).

Female and male flowers of *Limnobium* have an outer reflexed perianth whorl (Figures 2b and 2e) consisting of three, rarely four (in female flowers), purplish-tipped enrolled sepals. The petals in the alternating inner perianth whorl may be absent (Figure 2e), reduced to short rudiments (Figure 3e), *or* exceed by 1–2 mm the

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plant segment at anthesis; **e.** pistillate flower having 3 sepals, 0 petals, 3 awl-shaped staminodes (1-1-1 opposite sepals) and 12 hairy stigmatic lobes (6 deeply bifid stigmas); and **f.** lateral view of a mature elliptic pendent fruit without visible partitions in cross section, **g.** Cited specimen is deposited at UCMM.

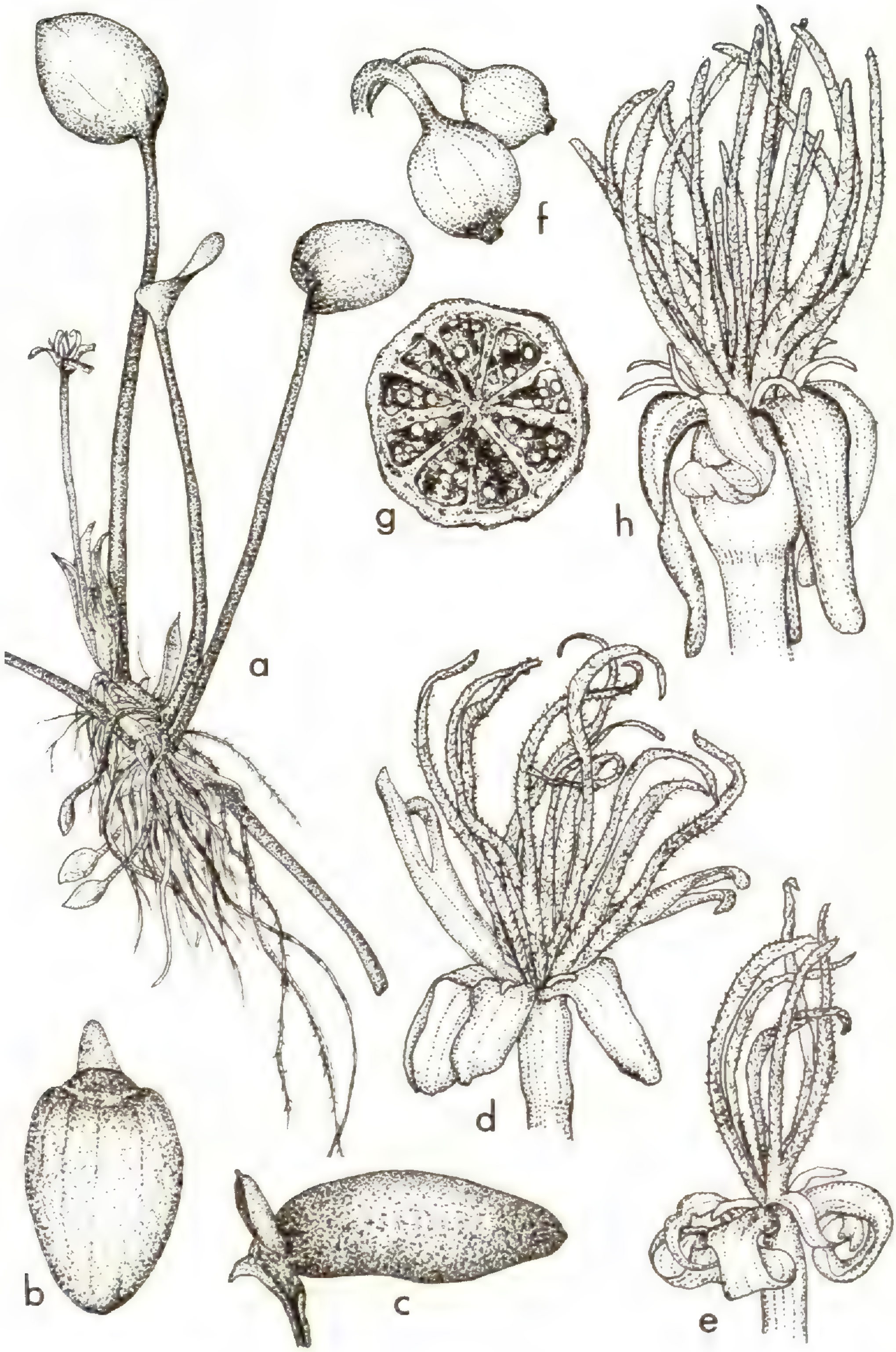

Figure 3. *Limnobium spongia* subsp. *laevigatum* (a)–(e): **a.–c.** from the Dominican Republic (*Lowden 3601*): **a.** leafy segments of a monoecious plant showing emergent rooted habit with staminate flower at anthesis and mature fruits of pistillate inflorescence borne on connective stolon; **b.** ventral and **c.** lateral views of floating juvenile plant propagators showing first true leaf and root; **d.** female

length of the sepals (Figure 4). Three erect whitish-mauve petals (Figure 4) characterize male flowers, whereas in female flowers there is an obvious reduction in the number and size of petals. In *Limnobium spongia* subsp. *spongia,* female flowers have three well-developed petals (Figure 3h), while in *L. spongia* subsp. *laevigatum* they show a conspicuous apetalous trend (Figures 2e and 3d–e).

Lobing of petals is also a significant trait in male and female flowers. The presence of unlobed petals predominates in both sexes of *Limnobium spongia* subsp. *spongia* (Figures 3h and 4a), whereas there are more bilobed petals (Figures 3d–e and 4b) and irregular petals with 3–4 minute lobes (Figure 4d) in *L. spongia* subsp. *laevigatum.* In this latter subspecies, bilobed petals appear to be more prevalent in male flowers, since fewer petals exist in female flowers due to apetaly.

Contrary to former reports (Kaul, 1968; Díaz-Miranda et al., 1981; Hunziker, 1982), my observations on male flowers reveal neither a constant number of stamens nor the absence of staminodes. A highly variable number of mucronate-tipped stamens (Figures 2c and 4) and awl-shaped staminodes (Figures 4a and 4c–d) make up the staminal column consisting of alternating trimerous whorls of connate staminal bases. These staminal parts (Figure 4) develop acropetally in the androecium where stamens or staminodes belonging to the first, third and fifth trimerous whorls are found opposite the sepals, while those in the second, fourth and sixth trimerous whorls are found opposite the petals. Stamens and staminodes become progressively smaller the higher up one moves on the staminal column, where eventually stamens may be reduced to staminodes that appear to be only anther-stalks (Figures 4a and 4c–d). In *Limnobium spongia* subsp. *spon-*

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flower from St. Lucia (*Lowden 3942*) having 3 sepals, 2 petals (deeply bifid), 4 staminodes (2 shown of 2-1-1 opposite sepals) and 11 stigmatic lobes (6 stigmas: 5 bifid and 1 unilobed); and **e.** a female flower from Argentina (*Lowden 3959*) with 3 sepals, 2 petals (1 bifid at tip), 3 staminodes (2 shown of 1-1-1 opposite sepals) and 6 stigmatic lobes (3 bifid stigmas).

Limnobium spongia subsp. *spongia* (f)–(h): **f.** two pendent globose fruits from Florida (*Lowden 3937*) showing in cross section, **g.** visible partitions of 9 pseudolocules; and **h.** female flower from Florida (*Lowden 3939*) having 3 sepals, 3 petals (2 shown), 7 staminodes (6 shown of 3-2-2 opposite sepals) and 17 stigmatic lobes (8 stigmas: 7 bifid and 1 trifid). Cited specimens are deposited at UCMM.

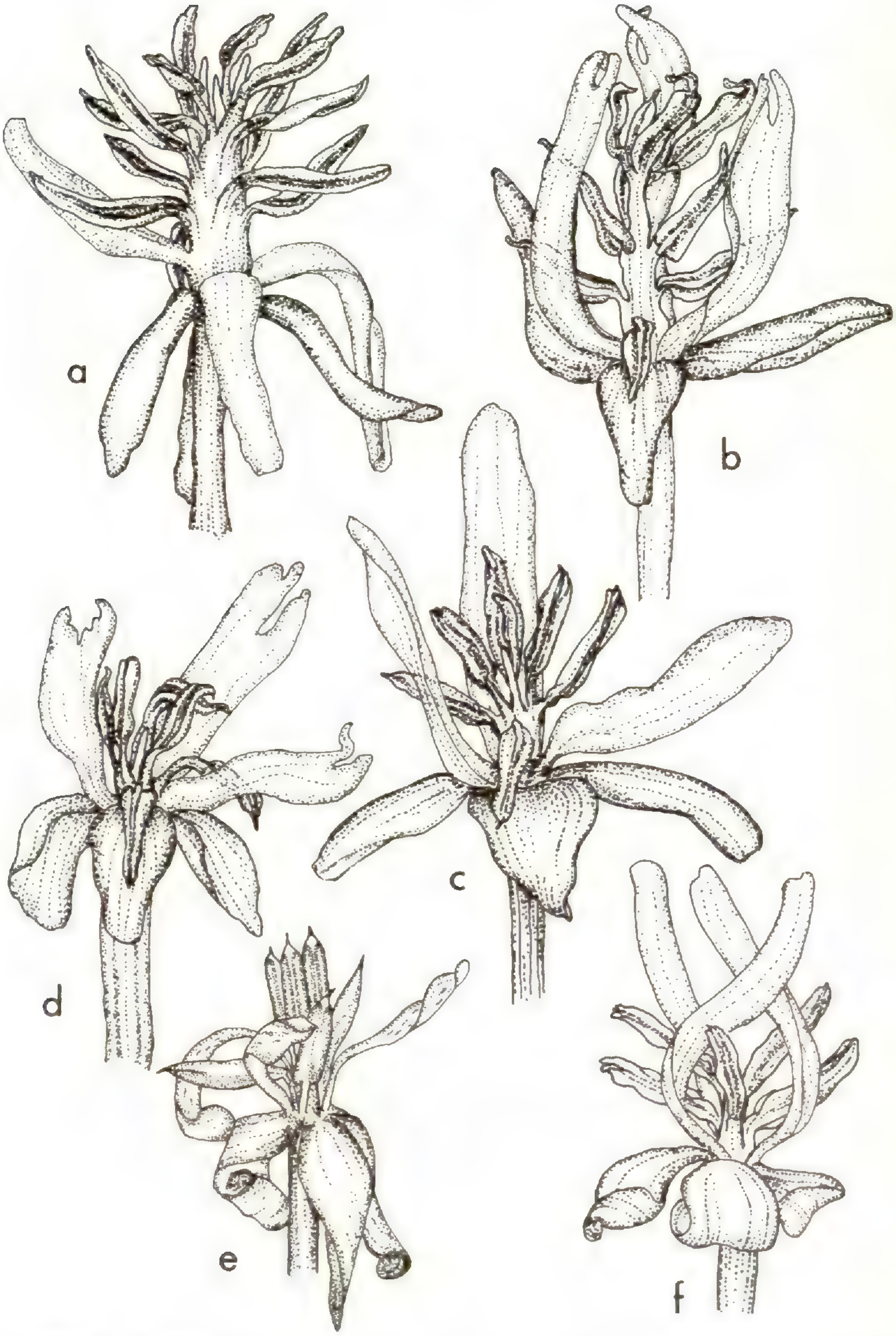

Figure 4. Floral parts in male flowers of *Limnobium spongia* subsp. *spongia* (a) and *L. spongia* subsp. *laevigatum* (b)–(f): **a.** 3 sepals, 3 unlobed petals and 13 fertile stamens with 3 staminodes from Illinois, U.S.A. (*Lowden 3948*); **b.** 3 sepals, 3 bilobed petals and 9 fertile stamens from the Dominican Republic (*Lowden 3947*); **c.** 3 sepals, 3 unlobed petals and 7 fertile stamens (7th just a half anther) with 1 staminode from Argentina (*Lowden 3952*); **d.** 3 sepals, 3 petals (varying

gia, the androecial column consists of 3–4 trimerous whorls of fertile stamens (Figure 4a), while in *L. spongia* subsp. *laevigatum* there are fewer fertile stamens (Figures 4b–f); just the first three trimerous whorls become filled. In northern latitudes the general tendency is toward twelve staminal parts in *Limnobium spongia* subsp. *spongia,* while in southern latitudes the trend is toward six staminal parts in *L. spongia* subsp. *laevigatum.* No real evidence was observed in fresh male flowers of pistillate parts along the central floral axis.

In female flowers no true stamens are found, only rudiments existing in one whorl as subulate antesepalous staminodes (Figure 2e). In both subspecies, these staminodes are frequently found in pairs. On the other hand, staminodes increase in numbers with a corresponding increase in the number of stigmatic lobes in *Limnobium spongia* subsp. *spongia* (Figure 3h), whereas female flowers with fewer stigmas have solitary staminodes opposite sepals in *L. spongia* subsp. *laevigatum* (Figures 2e and 3e). Even a true pistillate flower, without staminodes (Mosquera, Colombia; *Lowden 3929*), was observed in this latter subspecies.

The superior portion of the gynoecium in these imperfect female flowers consists of complete or incomplete alternating trimerous whorls having usually bifid stigmas (Figure 3e). Stigmas having one or three lobes occur infrequently. The three bifid stigmas (six stigmatic lobes) in the first (Figure 3e) and third whorls are found opposite the petals (if absent, then alternate with the sepals), while stigmas in the second trimerous whorl are found opposite the sepals and staminodes. In general, female flowers of *Limnobium spongia* subsp. *spongia* have more deeply bifid stigmas filling the second to the third trimerous stylar whorls, while fewer but somewhat less bifid stigmas fill just the first to the second trimerous stylar whorls in *L. spongia* subsp. *laevigatum.*

The inferior compound ovary bears few to many ovules borne on intruding parietal placental partitions formed by the connation of adjoining ventral carpel margins which show no signs of complete closure. The number of stigmas and placental projections is

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from 2–4 lobed) and 6 fertile stamens with 1 staminode from Colombia (*Lowden 3933*); **e.** 3 sepals, 3 unlobed petals and 6 fertile stamens from the Dominican Republic (*Lowden 3601*); and **f.** 3 sepals, 3 petals (2 slightly bilobed) and 5 fertile stamens from Argentina (*Lowden 3950*). Cited specimens are deposited at UCMM.

indicative of the number of fused carpels. The almost-closed carpels of the globose fruits (Figures 3f–g) in *Limnobium spongia* subsp. *spongia* have six to nine parietal placental divisions (pseudolocules), while the open carpels of elliptic fruits (Figures 2f–g) in *L. spongia* subsp. *laevigatum* have just one locule with usually three to six intruding parietal placentae.

An overall comparison of sexes in this monoecious plant (*Limnobium spongia*) reveals that male flowers more closely represent the imperfect state (unisexual), as evidenced by absence of pistillate parts, whereas female flowers present with great consistency an ancestral whorl of staminal rudiments opposite sepals, thus calling attention to a previous bisexual origin. Staminodes are well-developed in both sexes, yet frequently overlooked.

DIVERSITY IN POLLINATION MECHANISMS

Contrary to former belief (Cook, 1982; Cook and Urmi-König, 1983), the pollination mechanism in the genus *Limnobium* is not constant as in other genera of the Hydrocharitaceae. In this family, where the primitive nature of *Limnobium* is well known, it is not surprising to find a variety of pollination mechanisms (Hauman, 1915), depending on which floral modifications are present. As such, the sexual structures evolving in these imperfect flowers present a specialization in pollination mechanisms.

My field experience indicates that wind and insects appear to be the principal agents of pollination in both subspecies of *Limnobium spongia.* The slightest movement of the extended male pedicels (Figure 2a) brings down showers of sulfur-colored pollen onto the plumose stigmatic lobes of the shorter-stalked female flowers (Figure 2d). Powdery pollen masses reaching the water surface even float to stigmas of partially submerged female flowers. In nature, large numbers of minute aphid nymphs (*Aphididae*) and their predators, the Ladybird beetles (*Coccinellidae*), are frequent visitors that settle on the floral parts at anthesis.

Pollination by wind (anemophily) is most likely more effective in *Limnobium spongia* subsp. *spongia* where fertile stamens and stigmas are more abundant. On the other hand, in the more specialized flowers of *L. spongia* subsp. *laevigatum* insect (entomophily) and even surface pollinations might be more effective due to the reduction in the amount of pollen and stigmatic surfaces in these flowers having fewer sexual parts.

FLORAL VARIATION AND CHROMOSOME COUNTS

Cook and Urmi-König (1983) pointed out that in the Hydrocharitaceae, "one may find a greater degree of variation sometimes in a single species," such as in *Ottelia alismoides* (L.) Persoon which has "3–12 stamens, 3–10 carpels and may or may not develop dissepiments." They considered that this range of variation exceeded that found in *Limnobium.*

My field study reveals that *Limnobium* is just as, or even more, variable than *Ottelia alismoides. Limnobium spongia* has 3–14 stamens and 3–10 carpels with or without developed dissepiments. Considerable aneuploidy occurs in both of these species. As such, variation is even more accentuated in *Limnobium* where chromosome counts can be correlated with morphology and geography, while in *Ottelia alismoides* attempts to find correlations of this nature have failed (Cook and Urmi-König, 1984).

In *Limnobium* there exists a definitive relationship between character specialization, geographic latitude and chromosome number (Table 2). Significant differences in frequencies of floral variants for given population localities permit this overall formulation of male and female flower types in relation to known chromosome reports.

Chromosome counts (Table 2) elucidate an aneuploid series ($2n$ = 26, 27, 28, 29 and 30) in *Limnobium spongia.* In the northern range of the species, the base number of $x = 6$ has been reported from Paynes Prairie, Florida (Bernardello and Moscone, 1986). Here, the more primitive *L. spongia* subsp. *spongia* shows a relative constant diploid count of $2n = 24$, which corresponds with more stamens and staminodes in male flowers, while female flowers have more petals, stigmas and staminodes. On the other hand. chromosome counts from southern latitudes (Guadeloupe and Argentina) reveal plants with diploid complements of $2n = 26$–30. Frequencies for these counts (in parentheses) indicate a progressive increase in the diploid number as one goes further south where flower specialization is evidenced with fewer floral parts in plants of both sexes of *L. spongia* subsp. *laevigatum.* Supposing this to be the case, one would expect to find more counts of $2n$ = 30 in plants at the southernmost extreme of the distribution of this subspecies (Figure 1; San Miguel Del Monte, Argentina).

Further studies in the genus *Limnobium* should take into account the existence of these floral types in nature. In this manner, exact relationships might be established between cytotypes and

Table 2. Relationship between character specialization, geographic latitude and chromosome number in *Limnobium spongia*.

Subspecies	Overall Floral Type	Locality & Diploid Counts
Subsp. *spongia*	male: 12 stamens, petals 1-lobed female: 3 unlobed petals, 8–9 stigmas, staminodes 2–2–2 to 3–3–2	U.S.A.: Florida Paynes Prairie; $2n = 24$ (96 cells from 68 seedlings) (Bernardello & Moscone, 1986)
Subsp. *laevigatum*	male: 6 stamens, petals 1- 2-lobed female: 0–2 petals, 1–2-lobed; 5–6 stigmas; staminodes 1–1–1 to 2–1–1	Guadeloupe: West Island, Maire-Galante; $2n = 26(2), 27(6), 28(4), 29(2), 30(1)$ (Cook & Urmi-König, 1983)
	male: 6 stamens, petals 1–2-lobed female: 0–1 petals, unlobed; 5–6 stigmas; staminodes 2–1–1 to 2–2–1	Argentina: Córdoba—Cabalango & Embalse Río III; $2n = 28$ (75 metaphase plates from 51 plants) (Moscone & Bernardello, 1985)
	male: 6 stamens, unlobed petals, rarely 2-lobed female: 0–2 petals, 1-lobed, rarely 2-lobed; 5–6 stigmas; staminodes 1–1–1 to 2–1–1	Argentina: Buenos Aires, Riachuelo; $2n = 26(4), 27(3), 28(5), 29(5)$ (Cook & Urmi-König, 1983)

their corresponding morphological floral countertypes. Field experimentation between both subspecies of *Limnobium spongia* will most likely disclose the genetic pathways existing between floral traits and chromosomal germplasm. A better understanding of these cytological and morphological variation patterns in this primitive genus would undoubtedly extend our knowledge of phylogenetic trends in the Hydrocharitaceae.

TAXONOMY AND GEOGRAPHY

Limnobium L. C. Richard, Mém. Classe Sci. Math. & Phys. Inst. France (Paris), pp. 66–67, fig. 8. 1811 (pt. 2, publ. 1814).

Hydromystria G. F. W. Meyer, Prim. Fl. Esseq. 152–153. 1818.
Jalambicea Cervantes in De La Llave & Lexarza, Nov. Veget. Descr. 2: 12. 1825.
Rhizakenia Rafinesque, Autikon Botanikon, p. 188. 1840.
Trianea Karsten, Linnaea 28: 424. 1857.
Hydrocharella Spruce ex Bentham in Bentham & Hooker, Genera Plantarum 3(2): 452. 1883.

Plants monoecious (Fig. 3a), perennial aquatic herbs, stems trailing and rooted at nodes, leaves floating (aerenchymous) or aerial, blades rounded, cordate to spatulate, principal nerves converging (Figs. 2a & 2d). Flowers imperfect (Figs. 2b & 2e), inconspicuous, true petals white-mauve, in both sexes slightly longer and rarely as broad as the green-purplish sepals (Fig. 2b), apices narrowly rounded to irregularly lobed (Figs. 3d–e & 4), *or* petals reduced to rudiments or absent only in female flowers (Fig. 2e). STAMINATE FLOWERS (Fig. 4) with stamens and staminodes glabrous, united in one staminal column arising acropetally in alternating antesepalous or antepetalous trimerous whorls (Fig. 4b), anthers much longer than broad, mucronate-tipped (Fig. 2c). PISTILLATE FLOWERS (Figs. 2e, 3d–e & 3h) with staminodes glabrous, arranged in only one antesepalous whorl (Fig. 3h), stigmas bifid nearly to the base, exceeding the length of the perianth.

In the New World, the genus *Limnobium* might be confused in North America with the European frogbit, *Hydrocharis morsus-ranae* L., which has been introduced in Ontario and Quebec, Canada (Louis-Marie, 1958; Catling and Dore, 1982). Only recently, the European frogbit has spread from these Canadian provinces to New York (Roberts et al., 1981) where the American *Limnobium spongia* (Bosc) Steudel reaches its northern limits in the eastern United States (Figure 1). Despite their vegetative similarity, these two species are morphologically distinct, based on flower characters.

The European frogbit is a dioecious plant whose showy white-yellowish flowers have broadly-rounded petals that are much longer and broader than the sepals. In male flowers, the anthers of stamens are more or less oval, nearly as long as wide, bases of filaments are united in pairs, staminodes are hairy (at times so is the filament of the innermost stamen). In female flowers the antepetalous staminodes are glandular, while the antesepalous ones are elongate and hairy; stigmas are bifid for one-half their length and much shorter than the petals.

Limnobium is a monotypic genus, widely distributed in the temperate and tropical parts of the Americas.

TYPE SPECIES: *Limnobium spongia* (Bosc) Steudel

1. **Limnobium spongia** (Bosc) Steudel, Nom. Bot. ed. 2, 45. 1841. Type basionym: *Hydrocharis spongia* Bosc, Ann. Mus. Hist. Nat. Paris 9: 396–398, pl. 30. 1807. U.S.A., "Basse Caroline," *Bosc* (G, P).

Aquatic plants, floating to emergent, forming dense floating mats or inhabiting mudflats, roots fibrous, stems stoloniferous, nodes form leafy rosettes; leaves stipulate, rounded cordate or spatulate, green-purplish, entire, with 3–7 longitudinal nerves, cross-nerves less conspicuous, floating blades usually aerenchymous with short petioles, aerial blades with longer petioles and lacking a central spongy layer. Inflorescences cyme-like, sessile or short-pedunculate, subtended as flowers by floral (spathe) bracts, lanceolate to oblanceolate, few- to many-flowered, opening usually one at a time. Flowers unisexual, pedicels extended at anthesis, reaching approx. 11.0 cm in both sexes, sepals 3–4 (usually 3), boat-shaped, wider than petals, petals 0–4 (usually 3, except for the obvious apetalous trend in female flowers south of the United States), linear to lanceolate, slightly longer than sepals, unlobed or irregularly 2–4 lobed (2-lobed petals are not uncommon). STAMINATE FLOWERS with 3–14 fertile stamens (6 or 12 common), anthers approx. 4.0 mm long with mucronate tips, longitudinally dehiscing (Fig. 2c), 0–6 awl-shaped staminodes (if present, usually one), approx. 0.5–4.0 mm long. PISTILLATE FLOWERS with 0–4 antisepalous staminodes (usually 1–2), awl-shaped, reaching 4.0 mm long, 3–10 bifid hairy stigmas (6–19 stigmatic lobes), however, 5–6 are common (10–12 stigmatic lobes). Fruits pendent, beaked at apex, elliptic to globose (Figs. 2f & 3f), many seeded, berry-like, unilocular, placentation parietal, 3–9 intruding placental partitions, mature seeds beaked and covered with trichomes, approx. 0.1–0.3 mm long, seedling propagators (Figs. 3b–c) floating and inconspicuous.

In the Americas, *Limnobium spongia* occupies a variety of ecological habitats ranging from ponds, lagoons, swamps and lakes along hilly coastal plains at sealevel to mountain plateaus reaching 3000 m (Bogotá, Colombia). However, there is apparently no

variation in plants because of the change in altitude. Other aquatic plants commonly associated with *Limnobium spongia* are *Eichhornia crassipes* (Mart.) Solms, *E. azurea* (Sw.) Kunth, *Pistia stratiotes* L., *Lemna* spp., *Wolffiella* sp., *Nelumbo lutea* (Willd.) Pers., *Nymphaea* spp., *Azolla* sp., *Salvinia* sp. and *Ricciocarpus* sp.

KEY TO THE SUBSPECIES OF *LIMNOBIUM SPONGIA*

1a. Leaves cordate-based (especially in juvenile and floating blades) to rounded; fruits globose, 6–9 placental divisions; female flowers usually with 3 petals, number of bifid stigmas usually 6–9 (i.e., 12–18 stigmatic lobes); male flowers frequently have 12 fertile stamens (9–11 stamens not uncommon) ..... *L. spongia* subsp. *spongia*

1b. Leaves spatulate (rarely cordate based in floating blades); fruits elliptic, 3–6 intruding parietal placentae; female flowers without petals *or* if present usually less than 3, number of bifid stigmas commonly 4–6 (i.e., 8–12 stigmatic lobes); male flowers frequently have 6 fertile stamens (7–9 stamens not uncommon) ..... *L. spongia* subsp. *laevigatum*

In general, plants are larger in *Limnobium spongia* subsp. *spongia* as compared with a decrease in size and increase in number of plants per unit area in *L. spongia* subsp. *laevigatum.* Big aerial plants of the American frogbit, *L. spongia* subsp. *spongia,* reach the height of mature water hyacinth (*Eichhornia crassipes*) in rivers and lakes of Florida in the southeastern United States. Here, from the "St. John's River runs and lakes to Lake Okeechobee bays" (Bodle, 1986), these large plants of *L. spongia* subsp. *spongia* inhibit water flow or navigation and have been the target of an aquatic plant control program. On the other hand, in Colombia the smaller (less conspicuous) forms of *L. spongia* subsp. *laevigatum* flourish in drainage ditches where they recycle nutrients from wastewaters on the Bogotá Plateau.

In both subspecies there are exceptionally small flowering plants that inhabit mudflats in juxtaposition with larger aerial-flowering plants which normally float in entangled mats. The scarcity of these smaller flowering plants at northern latitudes made it impossible to determine further local relationships between plant

size and number of flower parts beyond those already established for the overall distribution of each subspecies.

1a. **Limnobium spongia** (Bosc) Steudel, subsp. **spongia**, Nom. Bot. ed. 2, 45. 1841. Type basionym: *Hydrocharis spongia* Bosc.

Hydrocharis spongia Bosc. Ann. Mus. Hist. Nat. Paris 9: 396–398, pl. 30. 1807. ["Basse-Caroline"]
Limnobium bosci L. C. Richard, Mém. Classe Sci. Math & Phys. Inst. France (Paris), pp. 32–34, fig. 8. 1814 (pt. 2, 1811).
Hydrocharis cordifolia Nuttall, Gen. North Am. Pl. 2: 241. 1818.

Plants taller (reaching approx. 5 dm), leaves with 5–7 principal nerves, secondary nerves usually visible, floating and aerial leaves cordate-based or rounded. Flowers of both sexes (Figs. 3h & 4a) usually with 3 well-developed unlobed petals (female flowers rarely with 2 or 4 petals; bilobed petals infrequent in both sexes). STAMINATE FLOWERS (Fig. 4a) with 8–14 (12 usually) fertile stamens and 0–5 staminodes (frequently one or even more present) in the upper (third through the sixth) trimerous whorls of an extended staminal column (Fig. 4a). PISTILLATE FLOWERS (Fig. 3h) with more (up to 4) staminodes in groups opposite sepals, staminodes robust, stigmatic lobes numerous (commonly 12–18). Fruits globose (Figs. 3f–g; approx. 1.0–1.6 cm wide) with 6–9 parietal placental divisions or pseudolocules; at maturity the outer ovary walls decay leaving partitions embedded in a gelatinous substance.

Throughout most of its distribution, this subspecies is a frequent inhabitant of swamps of bald cypress (*Taxodium distichum* (L.) Richard). Of particular interest was an herbarium specimen collected by Rogers (*Rogers, 8773-A*) from Rankin County, Mississippi. This dried specimen of a male flower has an unusual number of staminal parts: ten stamens and nine staminodes. The innermost structure extending from the staminal column appears to be a bilobed hairy stigma. Fresh material of male and female flowers from this particular locality might make it possible to ascertain the somewhat doubtful nature of this dried flower. Up until now, this male flower is the only one which I have seen with signs of a bisexual state.

DISTRIBUTION: (Figure 1.) This subspecies is endemic to temperate and subtropical regions in the United States where it mainly

occurs along the Gulf of Mexico and the Atlantic coastal lowlands from Louisiana-Florida-Delaware in the south, reaching a northernmost limit in the state of New York (Braddock Bay, Lake Ontario) in the northeast, extending to the southwest from the Mississippi River delta into Oklahoma and Texas, and in the Mississippi valley north to southern Illinois and southeastern Missouri in the midwest.

The unsubstantiated reports (Catling and Dore, 1982) from Monmouth County, New Jersey (Mackenzie, 1922; Fassett, 1957) and Lake County, Indiana (Deam, 1940) have not been included in this study, as well as specimens not seen by this author but cited by others for the states of Oklahoma (Langdon, 1959) and Kentucky (Catling and Dore, 1982).

1b. **Limnobium spongia** (Bosc) Steudel, subsp. **laevigatum** (Humboldt & Bonpland ex Willdenow) Lowden, *comb. nov.* Type basionym: *Salvinia laevigata.*

Salvinia laevigata Humb. & Bonpl. ex Willd., Sp. Pl. 5: 537. 1810. ["St. Fe de Bogotá"] (HOLOTYPE: B; ISOTYPE: P).

Hydromystria stolonifera G. F. W. Meyer, Prim. Fl. Esseq., 152–153. 1818 ["plantationis Hamburg," Guyana, Río Essequibo] (HOLOTYPE: GOET).

Jalambicea repens Cervantes in De La Llave & Lexarza, Nov. Veget. Descr. 2: 12. 1825. ["Frequentissima in defossis Mexicanis"].

Limnobium sinclairii Bentham, Bot. H.M.S. Sulphur 175. 1844. ["Guayaquil"] (HOLOTYPE AND ISOTYPE: K).

Trianea bogotensis Karsten, Linnaea 28: 424–425. 1857. ["in planitiei Bogotanae"] (ISOTYPE: US).

Limnobium stoloniferum (G. F. W. Meyer) Grisebach, Fl. Brit. West Ind. Isl. 506. 1862. ("Hab. Trinidad!, Cr.; [Guiana!]")

Hydrocharella echinospora Spruce ex Bentham in Bentham & Hooker, Gen. Pl. 3(2): 452. 1883. Brasil, ["flum. Amazonum. ad ostium flum. Solimoes"], *Spruce 1593* (HOLOTYPE: BM; ISOTYPES: G, K).

Hydrocharis stolonifera (G. F. W. Meyer) O. Kuntze, Rev. Gen. Pl. 3(3): 297. 1893. ["Concepcion de Paraguay"].

Hydromystria sinclairi (Bentham) Huaman, Anales Mus. Argent. Ci. Nat. "Bernardino Rivadavia" (Buenos Aires) 27: 326–327. 1915.

Limnobium bogotense (Karsten) Delay, Bull. Soc. Bot. France 88: 481. 1941.

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Limnobium laevigatum (Humb. & Bonpl. ex Willd.) Morton, Contr. U.S. Nat. Herb. 38: 270. 1973.

Hydromystria laevigata (Humb. & Bonpl. ex Willd.) A. T. Hunziker, Lorentzia 4: 5–8. 1981.

Hydromystria laevigata (Humb. & Bonpl. ex Willd.) Diaz-Miranda et al., Bot. J. Linn. Soc. (London) 83(4): 318. 1981.

Plants shorter (Figs. 2a, 2d, & 3a; reaching approx. 4.5 dm), leaves (Fig. 3d) with 3–5 principal nerves, secondary nerves inconspicuous, floating and aerial leaves (Figs. 2a & 2d) spatulate, rarely cordate-based. Only male flowers (Fig. 2b) usually with 3 petals (2 or 4 petals occur), while in female flowers petals reduced in size and number to the point where apetaly is common (Fig. 2e). In both sexes bilobed petals (Figs. 3d & 4b) are generally just as pronounced as unlobed petals (with an increase to 3-lobed and 4-lobed petals in female and male flowers, respectively. STAMINATE FLOWERS (Figs. 2b & 4b–f) with 3–10 (6 usually) fertile stamens and 0–3 staminodes (frequently absent but when present, one is common) in the upper (second through the fourth) trimerous whorls of the shortened staminal column (Fig. 4e). PISTILLATE FLOWERS (Figs. 2e & 3d–e) with zero (rare) or few (up to 3) staminodes opposite sepals, staminodes weak, stigmatic lobes fewer (commonly 8–12). Fruits elliptic (Figs. 2f–g; approx. 1.0–1.5 cm long to 0.4–3.5 mm wide) with 3–6 intruding parietal placentae, unilocular.

On the Caribbean islands of Puerto Rico and Martinique, I did not find any populations. In Puerto Rico, urban developments have destroyed habitats at Loiza Aldea; sugar cane plantations now extend from Arroyo to Patillas, just as rice fields and cattle pastures predominate from Vega Alta to Vega Baja and Florida. In Martinique, the ponds amongst the coastal hills have dried up and the Caravelle Peninsula today supports only a very dry bush vegetation affected by the encroaching sugar cane fields and livestock.

Deserving special mention are those herbarium materials that helped to delineate the geographic limit of *Limnobium spongia* subsp. *laevigatum* in Middle America. The drawing of the Mexican plant (*Sesse & Mocina,* F) shows clearly a male flower with 6 stamens and a female flower with 12 stigmatic lobes. Male specimens from Nicaragua (*Nichols 1058,* MO), El Salvador (*Roh-weder,* GH) and Costa Rica (*Crow & Charpentier 5933,* MO) have one, two or three bilobed petals, respectively, and 6 fertile stamens. Only the specimen from El Salvador has in addition one staminode. In the Greater Antilles, a Cuban specimen (*Leon 9032,* NY) disclosed diagnostic data for both sexes. The female flower has zero petals, 4 staminodes, 6 bifid stigmas and an ovary without dissepiments, while the male flower has 7 fertile stamens. Spec-

imens from Puerto Rico show 6 stamens (*Britton & Britton 7949,* NY) and elliptic fruits (*Sintenis 5779,* MO).

DISTRIBUTION: (Figure 1.) This tropical to temperate (in southern latitudes and altitudes) subspecies is found throughout the West Indies on the Caribbean islands of Cuba, Hispaniola (Dominican Republic) and Puerto Rico in the Greater Antilles, and Antigua, Montserrat, Guadeloupe, Martinique, St. Lucia and Trinidad in the Lesser Antilles; in Mesoamerica it mainly occurs along the Pacific lowlands of Mexico, Guatemala, El Salvador, Nicaragua, Costa Rica and Panama; and in South America it occurs in Colombia, Venezuela, Guyana, Surinam, French Guiana, Ecuador, Peru, Brazil, Paraguay, Uruguay and Argentina.

Worthy of mention are references to specimens from localities not personally examined but cited by other authors for Montserrat (Howard, 1979) and Trinidad (Simmonds, 1967). The existence of *Limnobium spongia* subsp. *laevigatum* in Guyana is based on the type specimen of *Hydromystria stoloniferum* ("Essequibo.") in the Grisebach Herbarium at Goettingen. Of further interest are reports of localities in southwestern Brazil (Hoehne, 1948: Corumbá and Cáceres, State of Mato Grosso), which lead one to expect further plant collecting in Brazil (Figure 1) will reveal a more than infrequent occurrence of this plant.

CONCLUSIONS

Plant collectors should recognize flower variants in nature and determine the number of flower parts along with their frequency of expression in populations. This relevant collection data should accompany locality information on herbarium labels. These kinds of field observations will be most helpful in understanding the real extent of variation in populations as compared to dried herbarium specimens which demonstrate none, or at most one, of these flower variants.

The dissemination of *Limnobium spongia* in the Americas appears to be through natural means instead of by artificial introductions. Perhaps this natural dissemination has contributed to the expression of a continuum in characters which may be observed as two diverging developmental patterns between North and South American latitudes. The overall similarity of flower

variants indicates that these developmental patterns have evolved from a common gene pool.

Inbreeding studies would be of great interest for experimentally determining the exact relationships between cytotypes and their corresponding morphological floral counterparts. Populations offer the diversity in flower variants, pollination mechanisms and cytotypes that make *Limnobium spongia* an attractive laboratory organism for a better understanding of species specialization and its phylogenetical implications in the Hydrocharitaceae.

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EL HERBARIO "RAFAEL M. MOSCOSO"
PONTIFICIA UNIVERSIDAD CATOLICA MADRE Y MAESTRA
FACULTAD DE CIENCIAS Y HUMANIDADES
SANTIAGO DE LOS CABALLEROS
REPUBLICA DOMINICANA (ANTILLAS)

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CHLORIS BARBATA SW. AND *C. ELATA* DESVAUX (POACEAE), THE EARLIER NAMES FOR *C. INFLATA* LINK AND *C. DANDEYANA* ADAMS

JOHN T. KARTESZ AND KANCHEEPURAM N. GANDHI

ABSTRACT

Andropogon barbatus L. 1759 and 1760 refer to a Jamaican grass, whereas *A. barbatus* L. 1771, a later homonym, applies to an East Indian grass. *A. polydactylon* L. 1763, a renaming of *A. barbatus* L. 1759 and 1760, is a superfluous name. *Chloris barbata* Sw. 1797, which was based on *A. barbatus* L. 1771, must be considered to be a *nom. nov. C. barbata* Sw. and *C. elata* Desvaux are the earlier names for *C. inflata* Link and *C. dandeyana* Adams.

Key Words: *Andropogon barbatus, A. polydactylon, Chloris barbata, C. dandeyana, C. elata, C. inflata, C. polydactyla*

INTRODUCTION

In his monograph of the genus *Chloris* Sw., Anderson (1974) used *C. dandeyana* Adams instead of *C. elata* Desvaux [found in Florida, Mississippi, Texas? (see below), the Caribbean Islands, and South America] and *C. inflata* Link for *C. barbata* Sw. (widely distributed in warmer parts of the world; in North America, found in Texas and the Caribbean Islands). Anderson's treatment of *C. inflata* and *C. dandeyana* has been followed by Gould (in Howard, 1979), Kartesz and Kartesz (1980), Soil Conservation Service (1982), and Hatch et al. (1990). Although Anderson (in Gould, 1975, p. 328, in the protologue of *C. canterai* Arech.) considered Gould and Box's 1965 report of the occurrence of *C. polydactyla* (= *C. elata*) in Texas to be an error, Hatch et al. (1990) reinstated it for plants from Texas. Our analysis of the nomenclature follows.

CHLORIS BARBATA SW., AN EARLIER NAME FOR *C. INFLATA* LINK

Anderson (1974, p. 34–36) discussed the taxonomy and nomenclature of *Andropogon barbatus* L. (Linnaeus, 1759, p. 1305; 1760, p. 412; 1771, p. 302) and *A. polydactylon* L. (Linnaeus, 1763, p. 1483). Although the protologues of *A. barbatus* L. 1759, *A. barbatus* L. 1760, and *A. polydactylon* differed slightly from each other, Anderson demonstrated that the preceding three names

were based on the same Jamaican specimen. However, *A. barbatus* L. 1771 was based on an East Indian specimen, belonging to a different species of *Chloris*. Anderson (p. 36) considered *A. barbatus* L. 1771 as a later homonym. Since Swartz (1797, p. 200) based his *C. barbata* on *A. barbatus* L. 1771, Anderson rejected *C. barbata* Sw. and accepted *C. inflata* Link (published in 1821). Due to its wide distribution in the tropics, we decided to investigate its post-1974 nomenclatural literature. Without discussion of the nomenclature and without referencing Linnaeus, Ramamoorthy (in Saldanha and Nicolson, 1976, p. 715) used the name *C. barbata* Sw. for this complex found in South India, whereas Cope (1982, p. 123) mentioned the illegitimacy of *A. barbatus* L. 1771 and used the name *C. barbata* Sw. for this species complex found in Pakistan. Our discussion follows.

Some workers may not accept the illegitimate status assigned to *Andropogon barbatus* L. 1771. Since it was Linnaeus himself who used the name *A. barbatus* for both the Jamaican grass and the East Indian grass, such workers may believe that Linnaeus misidentified the East Indian grass as the Jamaican grass and that *A. barbatus* L. 1771 is a misapplied name. Consequently, based on ICBN Art. 33 Note 1 (Greuter, 1988), such workers may treat *Chloris barbata* Sw. as a new species (as suggested by one of the anonymous reviewers of this article). However, we refute this view, with the following discussion provided.

First, in 1763, Linnaeus abandoned his binomial *Andropogon barbatus* L. 1759, and renamed it as *A. polydactylon*. We speculate that Linnaeus preferred the epithet *polydactylon* (= many fingers, referring to the 7–15, palmately arranged spikes) over the epithet *barbatus* (= bearded, perhaps referring to the pubescence of the lemma) for the Jamaican grass; nevertheless, the name *A. polydactylon* is superfluous. Second, in 1771, based on the belief that the epithet *barbatus* was still available for use in *Andropogon* L., Linnaeus proposed the name *A. barbatus* for a new East Indian grass. The protologue of *A. barbatus* L. 1771 is wholly different from those of *A. barbatus* L. 1759, *A. barbatus* L. 1760, and *A. polydactylon,* and has no direct or indirect reference to any of these protologues. Linnaeus' 1771 publication (titled *Mantissa*) mostly included additions to his previous publications; hence, Linnaeus did not list *A. polydactylon* in his *Mantissa*. However, Willdenow (1806, p. 926–927), who revised Linnaeus' *Species Plantarum,* recognized both *Chloris barbata* and *C. polydactyla*

as two distinct species. We assert that Linnaeus did not misidentify the East Indian grass, but correctly recognized it as a new species, distinct from *A. polydactylon.* Had Linnaeus, in 1763, not renamed *A. barbatus* L. 1759 as *A. polydactylon,* or had Linnaeus, in the protologue of *A. barbatus* L. 1771, referenced any of the three earlier works, then *A. barbatus* L. 1771 could be classified as a misapplied name, but that is not the case here. Hence, *A. barbatus* L. 1771, which was based on a type different from that of *A. barbatus* L. 1759, must be classified as a later homonym, and thus illegitimate. *Chloris barbata* Sw. must be treated neither as a new species nor as a new combination, but rather as a *nom. nov.* (without parenthetical authorship), with its priority from 1795 (Art. 72 Note 1, Ex. 2). Regarding Anderson's rejection of *C. barbata* Sw., we speculate that he was unaware of Art. 72 of the Code. As a legitimate name, *C. barbata* Sw. 1797 has priority over *C. inflata* (established in 1821).

CHLORIS ELATA DESVAUX, AN EARLIER NAME FOR *C. DANDEYANA* ADAMS

Adams (1971, p. 408) remarked that the type of *Andropogon polydactylon* is the type of *A. barbatus* L. 1759; hence, the former name is superfluous, and thus illegitimate (Art. 63.1). Instead of transferring *A. barbatus* L. 1759 to *Chloris,* Swartz (1788, p. 26) transferred *A. polydactylon* (= *C. polydactyla*). At that time, usage of the epithet *barbata* in *Chloris* was not pre-empted, since the name *C. barbata* Sw. 1797 (for the East Indian grass) appeared nine years later. Hence, in 1788, Swartz had the opportunity to use the name *C. barbata* (instead of *C. polydactyla*) for the Jamaican grass. Moreover, according to the present Code (Arts. 55.1b, 63.2), Swartz ought to have adopted the epithet *barbata,* since he included the type of *A. barbatus* L. 1759 for his combination, but failed to do so. Had Swartz (in 1788) used the name *C. barbata* for the Jamaican grass, then (in 1797) he could have chosen a different name for the East Indian grass. We presume that Swartz decided to follow Linnaeus' 1763 and 1771 treatments and ignored the 1759 and 1760 treatments. Nevertheless, the name *C. polydactyla* is also superfluous, and thus illegitimate (Art. 63.1).

Nash (1898, p. 443–445) briefly discussed the nomenclature of this complex (including illegitimacy of *Andropogon barbatus* L.

1771) and made the combination based on *A. barbatus* L. 1759: *Chloris barbata* (L.) Nash. Thus, Nash also failed to realize that his combination was illegitimate due to the existence of *C. barbata* Sw. Alternatively, Adams proposed the new name *C. dandeyana* for the Linnaean names of 1759, 1760, and 1763. Apart from his new name proposal, Adams provided no discussion on the taxonomy of this complex.

In addition to accepting *Chloris dandeyana,* Anderson cited three taxonomic synonyms [*C. elata* Desvaux, Opusc. Sci. Phys. Nat. 73. 1831; *C. consanguinea* Kunth (Rev. Gram. 1: 89. 1829, *nom. invalid.*) Enum. Pl. 1: 264. 1833; and *C. arundinacea* Nees ex Steudel, Syn. Pl. Glum. 1: 207. 1854], all of which are legitimate and have priority over *C. dandeyana.* Of these three synonyms, *C. elata* is accepted here to be the legitimate name in place of *C. dandeyana.*

TAXONOMY

Chloris barbata Sw., Fl. Ind. Occid. 1: 200. 1797.

Andropogon barbatus L., Mant. Pl. 302. 1771, non L. 1759. TYPE LOCALITY: India. No. 1211.21 (LINN; microfiche!). On the right side of the type specimen, the following are found: "Konda-Pulli Rheed. Mal. XII. p. 95. t. 51." (on the top of the sheet) and a sketch (on approximately middle right edge of the sheet) of unrecognizable meaning. In South Indian languages (Tamil and Malayalam), the word Kondai refers to a tuft of woman's hair and the word pullu refers to grass. The remainder of the citation refers to Rheede, Hort. Malab. 12: 95, t. 51. 1693. However, none of these particulars are found in Linnaeus' *Mantissa.* It is most likely that these data were entered by later workers. According to Nicolson et al. (1988, p. 307), Lamarck (1785, p. 376) was the first to associate Rheede's element with *A. barbatus* L. 1771.

C. inflata Link, Enum. Pl. 1: 105. 1821. "Type grown in the Berlin Botanic Garden from seed said to come from 'California,' probably from Mexico" (Hitchcock, 1936, p. 134). The type at B was presumably destroyed during World War II. Reputedly, a fragment of the type exists at US (*fide* Anderson, 1974, p. 53).

Chloris elata Desvaux, Opusc. Sci. Phys. Nat. 73. 1831. TYPE LOCALITY: Brazil. (P).

Andropogon barbatus L., Syst. Nat. ed. 10: 2: 1305. 1759; Amoen. Acad. 5: 412. 1760, non L. 1771. TYPE LOCALITY: Jamaica. No. 1211.28 (LINN; microfiche!).

A. polydactylon L., Sp. Pl. ed. 2. 2: 1483. 1763, nom. illegit.

C. polydactyla Sw., Prodr. 26. 1788.

C. barbata (L.) Nash, Bull. Torrey Bot. Club 25: 443. 1898, non *C. barbata* Sw. 1797.
C. dandeyana Adams, Phytologia 21: 408. 1971.

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THE NORTH CAROLINA BOTANICAL GARDEN
DEPARTMENT OF BIOLOGY, COKER HALL
UNIVERSITY OF NORTH CAROLINA
CHAPEL HILL, NC 27599-3280, USA

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GEOGRAPHICAL DISTRIBUTION AND ECOLOGY OF LONG'S BULRUSH, *SCIRPUS LONGII* (CYPERACEAE) IN CANADA

NICHOLAS M. HILL AND MATS E. JOHANSSON

ABSTRACT

Scirpus longii is a rare coastal plain plant traditionally regarded as a New Jersey Pine Barrens species. It had been known from only one site in Canada, in Nova Scotia, until it was recognized in its vegetative state. In Nova Scotia, *S. longii* occurs in wetlands where the importance of competition from shrubs has been reduced either by ice scour or flooding. Flooding, and consequent anaerobiosis, appears to be the main mechanism which reduces shrub growth in most *S. longii* habitats, but ice scour may be a more important factor on the shores of high watershed area lakes. *Scirpus longii* forms circular clones at all non-ice-scoured habitats. Above-ground production of shoots is restricted to the periphery of circular clones. Our data indicate that this circular phalanx may help the species to compete with shrubs. Populations in Nova Scotia appear to be secure; however, their persistence will be influenced by any factor which alters their competitive dynamics with shrubs.

Key Words: *Scirpus longii,* Long's bulrush, rare plants, shrub competition, flooding, clonal plants, circular growth, coastal plain flora, Nova Scotia

INTRODUCTION

Scirpus longii Fern., or Long's bulrush, was given specific status by Fernald (1911) after Bayard Long called his attention to an atypical *Scirpus* resembling *Scirpus atrocinctus* Fern. At that time, *S. longii* was known from "marsh" in the *Pinus rigida*-dominated barrens of New Jersey, and from meadow bordering the Charles River in Massachusetts. The species is listed as Imperiled by the Nature Conservancy, a ranking which is supported in a recent report by Rawinski (1990). This report stated that the species is most abundant in the Pine Barrens of New Jersey and is poorly represented in New England (Massachusetts, Rhode Island and New Hampshire), but that new findings from Maine show that wetlands bordering the Saco River support large *S. longii* populations.

The Canadian distribution rested upon Weatherby's report of a single population of *Scirpus longii* in Nova Scotia (1942). This report was not further investigated until 1988, when Hill and Keddy (1992, in press) discovered two new sites during an extensive survey of rare coastal plain plants. At several locations in

Nova Scotia, the distribution of *S. longii* and other globally-rare species (viz.: *Lophiola aurea* Ker-Gawl. and *Lachnanthes caroliniana* (Lam.) Dandy) overlap; our findings for a portion of the species' range of greatest value for conservation are included in Wisheu et al. (1992, in press). In this paper, we report the full distribution of *S. longii* in Nova Scotia, a species which was a distribution pattern typical of many Atlantic coastal plain species (Roland and Smith, 1969). We describe and attempt to classify the types of wetland habitat which support the species, and infer what environmental factors may be regulating the distribution.

METHODS

Identification

Initially, *Scirpus longii* could not be found among 47 Nova Scotian lakes surveyed in 1988 for rare Atlantic coastal plain plant species (Hill and Keddy, 1992, in press), despite the fact that it was documented to occur at one of these lakes. When unidentified vegetative shoots of a sedge were compared with those belonging to *S. longii,* it was realized that *S. longii* occurred in several locations but did not flower. Schuyler (1963a) noted this phenomenon in *S. longii* in New Jersey and observed that flowering culm formation was rare except after fires. It is essential to be able to identify the plant in its vegetative state. Rhizomes of *S. longii* are longer lived and consequently stouter (usually 1.5–3 cm diam.) than those of *S. cyperinus* (L.) Kunth or *S. atrocinctus* (usually 1–1.5 cm diam.). In Nova Scotia, *S. longii* grows under conditions of low disturbance as large circular clones commonly .75 to 5 m in diameter, although we have observed clones up to 50 m in diameter. In contrast, *S. cyperinus* rhizomes decay rapidly and small tussocks are formed (Schuyler, 1963b), usually less than 50 cm in diameter. At rich, mucky sites, the vegetative shoots of *Carex rostrata* Stokes ex With. may be confused with those of *S. longii*; however, *C. rostrata* does not form superficial rhizomes or large circular clones.

Once it became possible to identify vegetative *Scirpus longii,* the bogs and fens of the Medway and Tusket Rivers were investigated in 1989 and 1990. Two other sites in southwestern Nova Scotia were discovered in 1990 while doing inventories of bogs.

Distribution of *Scirpus longii* in Bogs

Scirpus longii was discovered in five types of wetlands which can be categorized as stillwater meadow, fen, "bay" and "barrier" bogs associated with lakes or rivers, and peaty lakeshores (described below). The within-bog distribution was studied at a lake "bay" bog at Shingle Lake. The relationship between cover of *S. longii,* water-logging and shrub growth was examined along five 50-m-long transects spaced at 10-m intervals. Transects ran from the lake edge of the bog inland to the rocky upper margin of the bog. Vegetation cover estimates were recorded according to the Braun-Blanquet scale and were transformed according to Maarel (1979). At each point along the transect, depth of standing water was recorded after sphagnum and litter were compressed.

Measurements of depth to the watertable were made at three hollows in the fen at Eighteen Mile Brook on August 20, 1990. Twenty-cm-diameter holes were excavated to depths below the watertable and depth from the surface peat to the watertable was determined after five minutes.

Vegetation Associated with Circular Clones

Clones of *Scirpus longii* are usually circular, above-ground shoots are restricted to the perimeter of the clone which gives them a "doughnut"-shaped appearance. Shrub growth was markedly lower in the interior region of clones than it was in the zone immediately outside the perimeter of leafy shoots of *S. longii.* We documented this phenomenon by measuring shrub height and cover in the interior region of clones of *S. longii* (Figure 2a, zone A) and in a ring-shaped area outside the perimeter of the leafy *S. longii* phalanx (Figure 2a, zone B). Dimensions of the outer ring area were calculated in the field so as to approximate the circular area surveyed inside the phalanx by considering the outer ring area to be a rectangle whose width was calculated by dividing the area of the interior circle by the outside circumference of the clone. Average error between these two sample areas (i.e., the interior circle and outer ring) for 21 circular colonies was 4.8%.

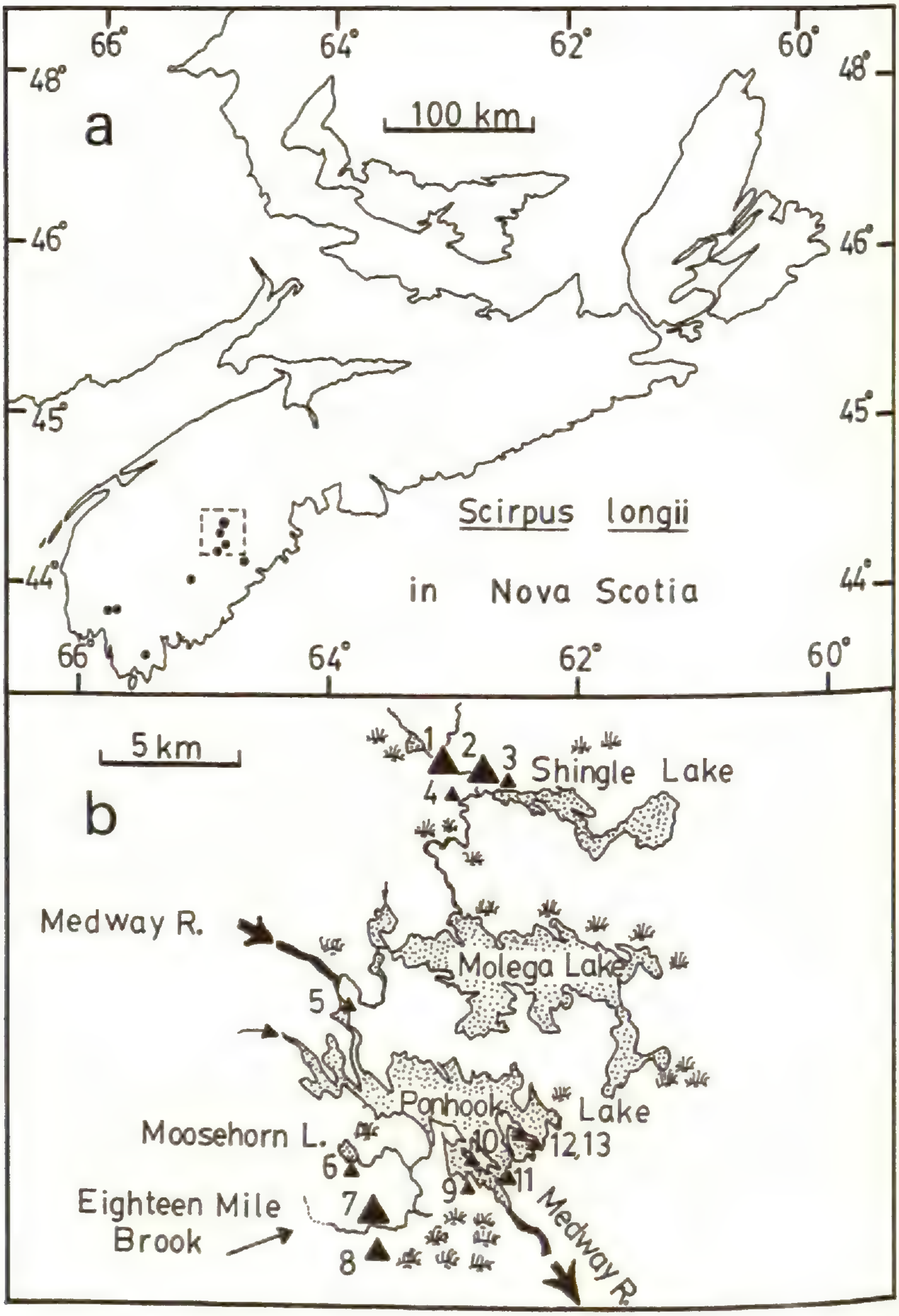

Figure 1. **a.** Distribution map of *Scirpus longii* in Nova Scotia. b. Map of above inset area showing sites in the Medway River watershed where *S. longii* is a dominant species over 10–15 ha. (▲), over 5 ha. (▲), and in less than 1 ha. (▲).

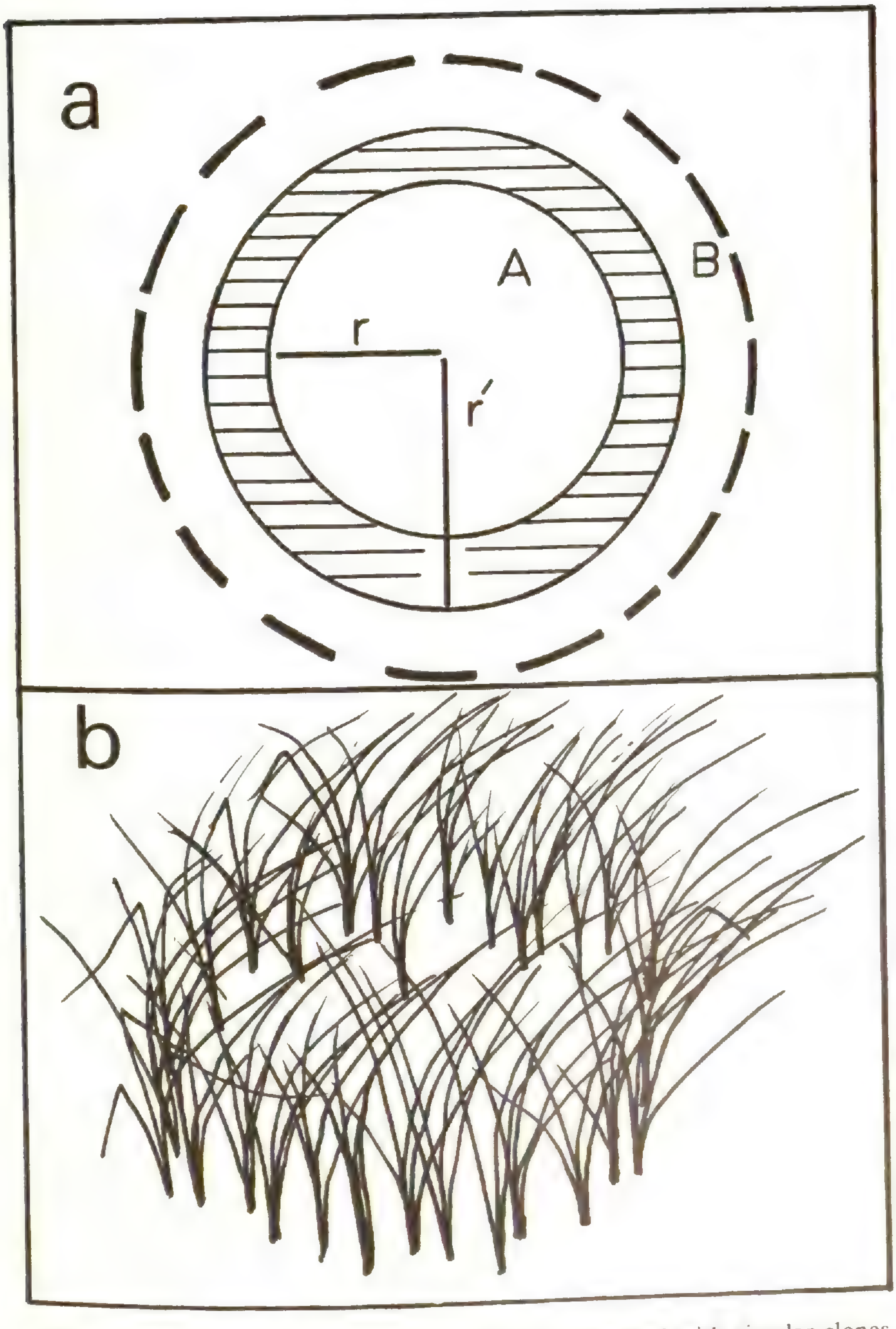

Figure 2. **a.** Sampling scheme for vegetation associated with circular clones of *Scirpus longii*: A = interior region, B = outer ring-shaped area surrounding the hatched region which represents the phalanx of *S. longii* shoots. Measurements used to obtain equivalent areas for A and B are r′, clone radius; and r, distance from the inside margin of the vegetated phalanx to center of clone. **b.** Simplified representation of outer phalanx of a class 1 clone (1 m diam.) of *S. longii* (positions of shoots traced from photograph of clone).

RESULTS AND DISCUSSION

Wetland Habitats of *Scirpus longii*

At all of the wetland habitats supporting *Scirpus longii* in Nova Scotia, *S. longii* grows on peat, but the hydrology of the sites varies greatly. Stillwater meadows border slowly-moving, tea-colored rivers at the outflow of Shingle Lake; they become inundated as water levels rise in winter and may remain flooded until late May. The sizes of large, discrete circular clones of *S. longii* in these stillwater meadows range from .75 m diam. (smaller, intact circular clones have not been found) to 20 m diam. The stillwater meadow is dominated by a matrix of graminoids (largely *Carex stricta* Lam., *C. oligosperma* Michx., *C. bullata* Schkuhr and *Spartina pectinata* Link), and contains large discrete clones of *S. longii* and the shrubs *Myrica gale* L. and *Salix pedicellaris* Pursh.

The "fens" bordering Eighteen Mile Brook have a more diverse shrub community scattered throughout hummock and hollow microtopography, with small trees (< 2.5 m) of *Acer rubrum* and *Larix laricina* and discrete circular clones of *Scirpus longii* which range from .75 m to 10 m in diameter. These fens are flooded in winter, but in summer the watertable drops 15–20 cm below the peat surface in hollows.

Lakeshore and riverside "bogs" can be classed either as "bay bogs" or "barrier bogs." Bay bogs form when peat accumulates in sheltered bays of lakes, eventually filling in the entire bay. Tall *Myrica gale* dominates the water's edge of these bay bogs, but shrub growth is depressed in the central waterlogged region behind the tall shrub zone. Shrub height and cover recovers toward the terrestrial rocky margin of the bay bog, which is the original lake shoreline. *Scirpus longii* is most commonly found in the central region of bay bogs, where the amount of standing water is greatest.

"Barrier bogs," on the other hand, are small wetland areas separated from lakes (or rivers) by a rocky barrier; they become flooded in winter when the water level of the neighboring waterbody rises. Because of the impermeable barrier of rock, these bogs remain flooded after the water level of the lake or river has fallen in spring. Muskrats have overwintered at both barrier bogs supporting *Scirpus longii,* and consume its culm base/rhizome region.

Unlike the foregoing boggy habitats where *Scirpus longii* ap-

pears to be restricted to waterlogged depressions away from the actual lake shoreline, at high watershed area lakes, populations of *S. longii* do occur directly on the peaty shores of lakes near the water's edge. Populations at the south of Ponhook Lake consist mainly of scattered clumps of less than 20 individual ramets which appear to be the remnants of larger clones fragmented by ice scouring. Such clumps occur most often on the downstream side of promontories at the outflow to Ponhook Lake. In contrast, at Lac D'Ecole and at Little Ponhook Lake (a small embayment of Ponhook Lake), discrete, intact circular clones of *S. longii* occur at the water's edge in peaty muck. Interestingly, judging from the lake size and the amount of mucky organic matter on respective shorelines, it appears that these populations experience less ice scour than is normal on the shorelines of high watershed area lakes.

We do not know yet how old the clones are at these various sites. Large clones of 5 m or more in diameter occur only in the extensive peatland sites, the stillwater meadows and the fen beside Eighteen Mile Brook. The smallest clones occur directly on the peaty shores of high watershed area lakes. This pattern suggests that extensive clone development may occur only where disturbance is minimal.

New Occurrences of *Scirpus longii*

We confirmed that *Scirpus longii* still occurs at Ponhook and Moosehorn Lakes (Figure 1, sites 6 and 9–12). Weatherby (1942) had documented its occurrence at Ponhook Lake and had found "a battered individual, probably of this species" at Moosehorn Lake. We found only four small clones (each < 1 m in diameter) of *S. longii* at the boggy outflow of Moosehorn Lake. At Ponhook Lake, several small populations (each with less than 1000 individual ramets) occur on the peaty shore of the lake. Large populations (> 5000 individual ramets) occur at site 9 in marsh beside the lake; the largest of these populations occurs over one hectare of a bay bog where approximately 200 clones contain an estimated total of 40,000 individual ramets (systematic sampling over gridded area).

Once we were able to identify non-flowering clones of *Scirpus longii* (primarily from their circular growth form and their stout

superficial rhizomes), we discovered that the largest populations of *S. longii* in Nova Scotia had gone unnoticed and occur over about 25 ha of stillwater meadow near Shingle Lake (Figure 1, sites 1 and 2), and in 15 ha of fen beside Eighteen Mile Brook (Figure 1, sites 7 and 8), where they rarely produce flowering culms. Weatherby had not visited Shingle Lake in 1941, but did visit the fen at Eighteen Mile Brook where he recorded *Salix pedicellaris* var. *hypoglauca*. The fen must have had quite a different aspect in 1941. Judging from our preliminary estimates of the annual radial expansion rate of *S. longii* (4 cm $yr.^{-1}$), and assuming that established clones have a low mortality rate, only the few clones that are now two meters in diameter would have been present in 1941.

All of the lakeshore bogs we found supporting *Scirpus longii* in Nova Scotia are quite small ranging from .1 to 1 ha. In addition to those reported for Ponhook Lake (Wisheu et al., 1992, in press), we have found *S. longii* in two lakeshore bay bogs and in one barrier bog at Shingle Lake (site 3), and in a barrier bog at Riversdale on the Medway River (discovered by C. Keddy and I. Wisheu).

The above sites for *Scirpus longii* belong to the Medway River watershed area. Lakes of this river system and of the Tusket River have the highest species richness of rare coastal plain plants in Nova Scotia. Many of the rare species are found in both river systems, but others are found in one river and not in the other (e.g., *Sabatia kennedyana* Fern. and *Coreopsis rosea* Nutt. in Tusket River, and *Lophiola aurea* and *Lachnanthes tinctoria* in Medway River). It appeared that *S. longii* might be restricted to the Medway watershed until we found two small populations on two lakes of the Tusket River, 80 km away from the closest site in Medway watershed. The population at Wilson's Lake (43°56′N, 66°53′W) is in a bay bog behind the water's edge line of shrub, while at Lac D'Ecole (44°56′N, 65°49′W) circular clones of *S. longii* grow at the water's edge on organic muck.

We have since discovered two isolated populations in fenland between the Medway and Tusket watersheds, at Dunraven Bog (44°05′N, 65°08′W) and at the southern end of Quinns Meadow (43°40′N, 65°29′W). The small population at Dunraven Bog appears stable, judging from the robust circular clones (ca. 1 m diam.) of *Scirpus longii,* but that at Quinns Meadow is composed of small groups of individual shoots (total 100) in a wet meadow

of *Carex bullata, C. stricta* and *C. oligosperma* which has been disturbed by all-terrain vehicles.

There are undoubtedly many other locations where *Scirpus longii* grows in Nova Scotia which have yet to be discovered. It is apparent that the province has not been thoroughly botanized; at two of the new sites for *S. longii* (Shingle Lake site 3 and Dunraven Bog), we found the endangered and showy *Lophiola aurea,* noticeable immediately to any field botanist, but hitherto unreported.

Relationship with Shrub Growth

At bay bogs on Shingle Lake and at Wilson's Lake, shrub height was greatest at the water's edge and at the terrestrial margin of the bog near the edge of woods (see Figure 3, Shingle Lake). Conversely, cover of *Scirpus longii* was greatest at the waterlogged central region of the bog, although this relationship was not significant due to the limited number of occurrences within the transect. Cover of *S. longii* in the Shingle Lake bog was significantly (t-test, $P = .05$) greater in areas without shrubs (.63 + 1.02, $\bar{x}$ + SD, $n = 19$) than in those with shrubs (.11 + .38, $\bar{x}$ + SD, $n = 46$).

The inverse relationship between shrub height and cover and of *Scirpus longii* found at this bay bog may be due to an inability of *Myrica gale,* the dominant shrub, to endure prolonged waterlogging. The same within-bog distribution of *S. longii* was observed at every bay bog whose lake margin was dominated by shrubs: standing water collected in their interior region where shrubs were sparse and *S. longii* most abundant. Similarly, at barrier bogs, *S. longii* was most abundant in the central, depressed region where the watertable is highest (standing water in center until mid-May) and shrub growth is lowest. Since shrubs grow vigorously at lake margins of bay bogs where there should be free exchange of oxygenated water between the lake and shrub roots, it may not be flooding per se which restricts shrub growth, but rather stresses associated with anaerobiosis (Jackson and Drew, 1984; Kozlowski, 1984; Dionigi et al., 1985).

Keddy and Wisheu (1989) have suggested that as a group, rare coastal plain plants are poor competitors and hence need to occupy habitats in which the importance of competition is reduced

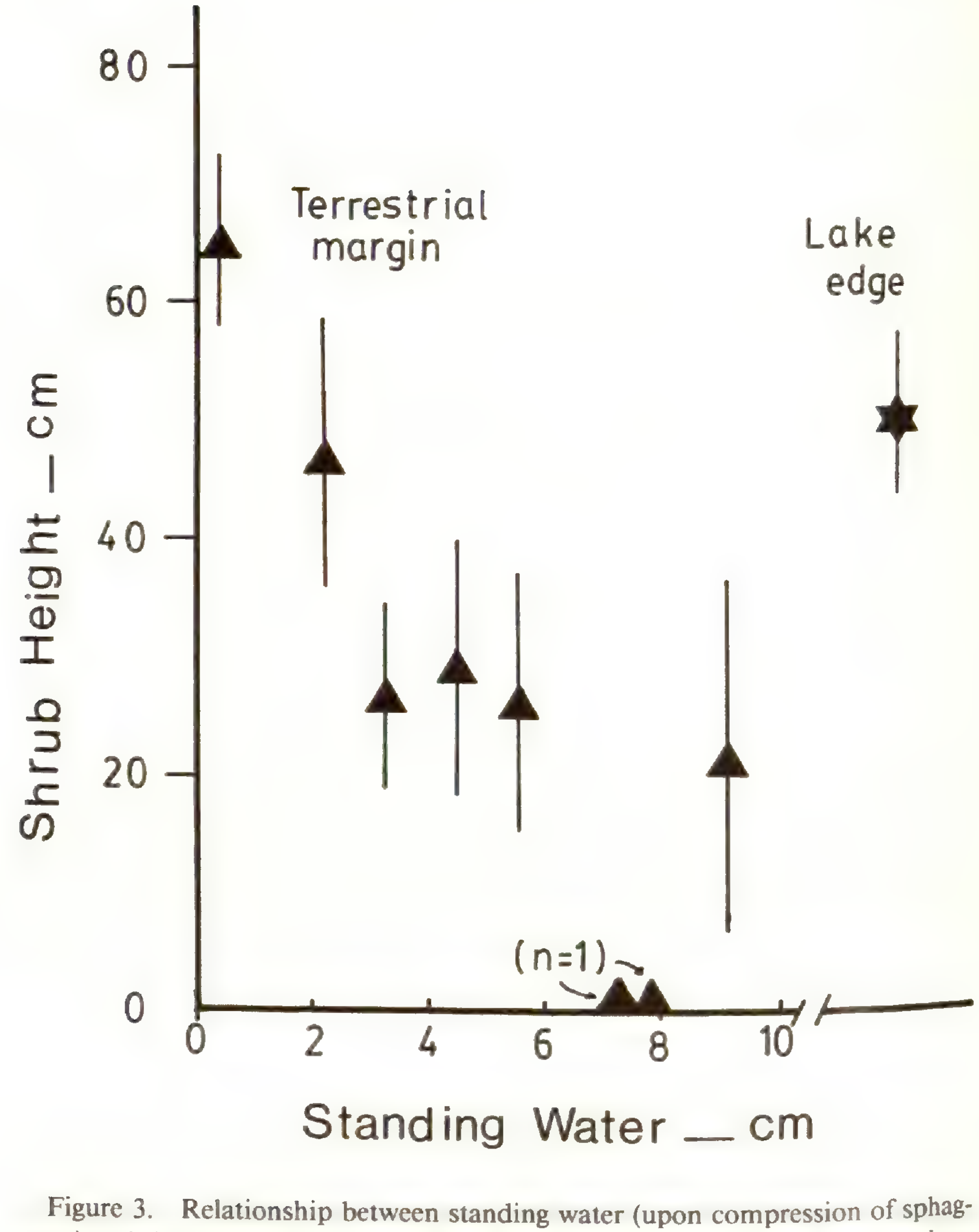

Figure 3. Relationship between standing water (upon compression of sphagnum) and shrub height for 65 positions along 5 transects of Shingle Lake bay bog. Note that the data point for lake edge starting positions is given a different symbol (★) and plotted off-scale on the X-axis because lake depth at the edge of the bog is much greater than the maximum standing water depth in the bog. Vertical bars represent standard errors of mean values.

by stress or disturbance (*sensu* Grime, 1979). *Scirpus longii* occurs in bogs and on peaty lakeshores where different mechanisms may permit it to avoid competition from shrubs; such shrubs appear to be eliminated from the shores of high watershed area lakes by

disturbance or stresses associated with flooding. Hill and Keddy (1992, in press) showed that richness of rare coastal plain plants was largely accounted for by watershed area, a measure which was strongly correlated with the over-winter flooding of lakes. *Scirpus longii* occurs in wetlands having a wide range of watershed areas, but it only occurs directly (i.e., not in a bog above the waterline) on the shores of high watershed area lakes (Ponhook Lake = 109,280 ha; Lac D'Ecole = 81,641 ha). The exact mechanism of how shrub growth is checked by flooding on the shores of high watershed lakes is not clear. One hypothesis is that there is greater ice scouring during the winter in areas where waterlevel fluctuations and river currents are greatest. In this case, ice scouring would not only remove nutrients from the site as litter is removed, but ice movement would sever above-ground growth. Although severe ice scouring could eliminate both shrubs and *S. longii* clones from lakeshores, zones of moderate scouring (e.g., in coves, behind promontories) can be observed on lakeshores where the above-ground woody shoots of shrubs have been largely removed, yet stout superficial rhizomes of other species remain. At such sites (e.g., 10 and 12 at Ponhook Lake), thick superficial rhizomes of *Osmunda regalis* are found with those of *S. longii*.

In contrast to populations of *Scirpus longii* at the water's edge of high watershed lakes, it appears that in bogs it is local rather than regional hydrology which determines distribution of the species. In bay and barrier bogs, water movement between the depressed central region of the bog and the larger water body (lake or river) is limited; here, shrubs are protected from ice scour but their growth appears to be depressed by anaerobiosis.

Vegetation Association with Circular Clones

In areas of low disturbance, *Scirpus longii* clones are circular in outline, and above-ground shoots are confined to the periphery of the clone (Figure 2b). This growth pattern has been observed in *Spartina townsendii* H. & J. Groves (Caldwell, 1957) and in *Larrea tridentata* (Sesse & Moc ex DC.) Coville (Vasek, 1980). Bell and Tomlinson (1980) suggested that in the absence of specific environmental constraints, clone shape is innate and is determined by the precise rhizome branching pattern of the species in question. More specifically, Caldwell (1957) hypothesized that

Table 1. Vegetation structure inside and outside *Scirpus longii* clones of two size classes. Small clones range from 1–2.5 m; large clones from 5–6. Standard error appears in parenthesis below its mean value.

	Small Clones (n = 16)		Large Clones (n = 6)	
Vegetation	Interior	Outer Ring	Interior	Outer Ring
Shrub Height (cm)	12.20 (1.22)	17.40 (0.86)	20.00 (0.63)	29.20 (1.42)
Shrub Cover Units*	1.48 (0.36)	3.40 (0.36)	3.66 (0.50)	7.83 (0.32)
Species Richness**	6.31 (0.81)	8.38 (0.87)	16.7 (1.75)	21.2 (2.70)
S. longii Cover Units	0.44 (0.16)	0.38 (0.15)	2.67 (0.34)	0.17 (0.17)

* Braun-blanquet scale transformed according to Maarel (1979).

** All vascular plant species; inner and outer areas are equivalent for each class size.

circular growth patterns occur only in areas where the importance of competition is low. The circular form of *S. longii* clones observed in areas that we believe are flood-stressed (e.g., stillwater meadow, barrier and bay bogs) is consistent with Caldwell's hypothesis. Competitive interactions between *S. longii* and shrubs appear to be small at the most water-logged locations where shrub cover is low; however, we have observed what appears to be a physical interference between circular clones of *S. longii* and shrubs in fens, the driest of the *S. longii* habitats in summer.

Scirpus longii clones of ca. 1 m or more in diameter are circular and present an outer phalanx of attached litter and densely packed leafy shoots. Rhizome sections to the inside of the outer phalanx produce very few above-ground shoots (Figure 2b); however, this interior region of clones frequently has little shrub growth in comparison with that immediately to the outside of the leafy perimeters of *S. longii* clones. An indication of the possible interference of *Scirpus longii* of shrubs at Eighteen Mile fen was obtained by comparing the cover and height of shrubs in the interior region of circular clones (Figure 2a, zone A) with those measures in an equivalent ring-shaped area just outside the clone (Figure 2a, zone B). The height and cover of shrubs was markedly lower in the interior than in the outer ring (Table 1). Interestingly, the above-ground cover of *S. longii* in the interior region was less

than the cover of shrubs in this region (Table 1). Shrub cover and height were also lower in the interior region of large clones (5–6 m diam.); however, in this case, vegetative cover of *S. longii* was substantial in the interior region and may account for the reduction in shrub growth. With both small and large clones, total species richness was higher in the interior than in the exterior region of the clone (Table 1).

We do not know how small clones of *Scirpus longii* exclude shrubs from their barren interior regions. Preliminary investigations reveal that the rhizomes in the interior of the clones are mostly dead but that they persist and form a fretwork which is overlain by decaying litter and moss. Shrubs may be excluded in part by the outer leafy phalanx of *S. longii* shoots because shrub shoots invading the phalanx would have to establish their roots in layers of *S. longii* litter on top of the matrix of dead rhizomes. Shrub growth may also be reduced if soil nutrients in the clone interior have been depleted by *S. longii*.

Most of the wetland habitats occupied by *Scirpus longii* in Nova Scotia are not immediately threatened, but it is important that the high population density sites in fen and river meadow receive protection. Distributional evidence suggests that this plant conforms with the generalization that coastal plain plants require habitats where competition is reduced (Keddy and Wisheu, 1989). Alteration of bogland hydrology changes the vegetation (Larsen, 1982; Thibodeau and Nickerson, 1985), such changes may favor aggressive species to the detriment of coastal plain flora, as was observed in the New Jersey Pine Barrens (Ehrenfeld, 1983). The status of this plant in Nova Scotia could easily be made more secure by safeguarding the small watersheds of the stillwater meadow and fen sites which support the largest *S. longii* populations.

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N. M. H.
DEPARTMENT OF BIOLOGY
MOUNT ST. VINCENT UNIVERSITY,
HALIFAX, NOVA SCOTIA
CANADA, B3M 2J6

M. E. J.
DEPARTMENT OF ECOLOGICAL BOTANY
UMEÅ UNIVERSITY
S-901 87 UMEÅ, SWEDEN

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THE FLORA OF LIMESINK DEPRESSIONS IN CAROLINA BEACH STATE PARK (NORTH CAROLINA)

DAVID J. SIEREN AND KAREN R. WARR[1]

ABSTRACT

Seven selected limesink depressions in Carolina Beach State Park (New Hanover County, North Carolina) were floristically surveyed in 1990. One state record, 11 county records, and 28 species of special interest or concern are among the 108 vascular plant species collected or observed.

Key Words: Vascular plants, limesink depressions, distribution records, North Carolina

INTRODUCTION

As part of a general floristic survey of the vascular plants of Carolina Beach State Park (New Hanover County, North Carolina), seven selected limesink depressions were studied from January through December 1990. Such depressions are reportedly formed by the slumping of surface soils following fracture and dissolution of underlying limestone (McDonald et al., 1981; Taggart and Dickerson, 1980); those chosen exhibited a variety of types, from very dry to very wet, and with and without woods. For purposes of identification and description, the depressions were assigned the following names: (1) Sawgrass Pond (a small, elliptical depression ca. 29 m × 53 m at its widest points with a population of sawgrass in its center), (2) Loblolly Pond (a shallow, dry depression ca. 40 m × 56 m with numerous small loblolly pines scattered throughout), (3) Lily Pond (a large pond ca. 66 m × 150 m, normally aquatic with standing water and water lilies), (4) Cypress Pond (a partially wooded depression with numerous pond cypresses. This depression consists of east and west sections which in most years are separated by a dry ridge and which often have standing water in their centers. In wet years such as 1991, they can be one continuous pond; together they are ca. 61 m wide × 218 m long), (5) Dry Pond (ca. 25 m × 84 m, drier and more shallow than the others, usually without standing water), (6) Gum Pond (a nearly round depression ca. 48 m in diameter, partially

[1] Present address: 5385-J New Centre Dr., Wilmington, NC 28403

wooded with numerous pond cypresses and black gums), and (7) Grass Pond (ca. 41 m × 109 m, dominated by grasses and other herbaceous vegetation). All of the limesinks surveyed are surrounded by longleaf pine–scrub oak communities, and they grade from their moist or aquatic centers or low areas upward to surrounding xeric sand ridges, often having distinct vegetation zones with increasing elevation.

The limesinks were surveyed on 26 weekly trips, primarily during the active growing season, March through October; known species were recorded and unknowns were collected and identified. The 249 voucher specimens have been deposited in WNC; nomenclature follows that of Kartesz and Kartesz (1980). In the species list, synonyms from Radford et al. (1968) are given in brackets following those taxa with name changes.

SPECIES LIST

Pteridophyta

BLECHNACEAE

Woodwardia virginica (L.) Smith

LYCOPODIACEAE

Lycopodium alopecuroides L.
Lycopodium appressum (Chapman) Lloyd & Underwood
Lycopodium carolinianum L.

OSMUNDACEAE

Osmunda regalis L. var. *spectabilis* (Willd.) Gray

Gymnospermae

PINACEAE

Pinus taeda L.

TAXODIACEAE

Taxodium ascendens Brongn.

Angiospermae

ACERACEAE

Acer rubrum L.

ANACARDIACEAE

Toxicodendron radicans (L.) Kuntze. [*Rhus radicans* L.]

APIACEAE

Centella asiatica (L.) Urban
Oxypolis filiformis (Walt.) Britt.

AQUIFOLIACEAE

Ilex cassine L.
Ilex glabra (L.) Gray

ASTERACEAE

Coreopsis falcata Boynt.
Erechtites hieracifolia (L.) Raf. ex DC.
Eupatorium capillifolium (Lam.) Small
Eupatorium leptophyllum DC. [*Eupatorium capillifolium* var. *leptophyllum* (DC.) Ahles]
Eupatorium recurvans Small
Euthamia tenuifolia (Pursh) Greene [*Solidago microcephala* (Greene) Bush]
Pluchea rosea Godfrey

BROMELIACEAE

Tillandsia usneoides (L.) L.

BURMANNIACEAE

Burmannia biflora L.
Burmannia capitata (Walt.) Mart.

CAMPANULACEAE

Lobelia nutallii Roemer & Schultes

CLUSIACEAE [HYPERICACEAE]

Hypericum cistifolium Lam.
Hypericum reductum P. Adams

CYPERACEAE

Cladium jamaicense Crantz
Cyperus polystachyos Rottb. var *texensis* (Torrey) Fern.
Eleocharis equisetoides (Ell.) Torr.
Eleocharis melanocarpa Torr.
Psilocarya scirpoides Torr.
Rhynchospora chalarocephala Fern. & Gale
Rhynchospora chapmanii M. A. Curtis
Rhynchospora corniculata (Lam.) Gray
Rhynchospora filifolia Gray
Rhynchospora inundata (Oakes) Fern.
Rhynchospora pleiantha (Kükenthal) Gale
Rhynchospora plumosa Ell.
Rhynchospora tracyi Britt.
Rhynchospora wrightiana Boeckl.
Scleria georgiana Core
Scleria reticularis Michx. var. *pubescens* Britt.

CYRILLACEAE

Cyrilla racemiflora L.

DROSERACEAE

Drosera capillaris Poiret
Drosera intermedia Hayne

EBENACEAE

Diospyros virginiana L.

ERICACEAE

Lyonia lucida (Lam.) K. Koch
Lyonia mariana (L.) D. Don
Vaccinium corymbosum L. [*Vaccinium atrococcum* (Gray) Porter]

ERIOCAULACEAE

Eriocaulon compressum Lam.
Lachnocaulon beyrichianum Sporleder. ex Koern.

GENTIANACEAE

Bartonia paniculata (Michx.) Muhl.
Bartonia verna (Michx.) Muhl.
Sabatia difformis (L.) Druce

HALORAGIDACEAE

Proserpinaca pectinata Lam.

HAMAMELIDACEAE

Liquidambar styraciflua L.

JUNCACEAE

Juncus abortvus Chapman
Juncus scirpoides Lam.

LAURACEAE

Persea borbonia (L.) Sprengel.

LENTIBULARIACEAE

Pinguicula caerulea Walt.
Utricularia juncea Vahl.
Utricularia purpurea Walt.
Utricularia subulata L.

LINACEAE

Linum floridanum (Planch.) Trel. var *floridanum* [*Linum virginianum* L. var. *floridanum* Planch.]

MAGNOLIACEAE

Magnolia virginiana L.

MELASTOMATACEAE

Rhexia cubensis Griseb.
Rhexia mariana L. var. *mariana*

MYRICACEAE

Myrica cerifera L.

NYMPHAEACEAE

Nymphaea odorata Ait.

NYSSACEAE

Nyssa sylvatica Marsh var. *biflora* (Walter) Sargent

ONAGRACEAE

Ludwigia linifolia Poir.
Ludwigia suffruticosa Walt.

ORCHIDACEAE

Pogonia ophioglossoides (L.) Juss.

POACEAE

Andropogon capillipes Nash [*A. virginicus* L., in part]
Andropogon perangustatus Nash
Andropogon virginicus L. var. *virginicus*
Aristida affinis (Schultes) Kunth.
Aristida purpurascens Poir.
Aristida virgata Trin.
Coelorachis rugosa (Nutt.) Nash [*Manisuris rugosa* (Nutt.) Kuntze]
Dichanthelium acuminatum (Sw.) Gould & Clark var. *longiligulatum* (Nash) Gould & Clark [*Panicum longiligulatum* Nash]
Dichanthelium dichotomum (L.) Gould var. *ensifolium* (Baldw. ex Ell.) Gould & Clark [*Panicum ensifolium* Baldwin ex Ell.]
Eragrostis refracta (Muhl.) Scribn.
Erianthus giganteus (Walt.) Muhl.
Panicum rigidulum Bosc ex Nees [*Panicum agrostoides* Spreng.]
Panicum tenerum Bey. ex Trin.
Panicum verrucosum Muhl.
Panicum virgatum L.
Paspalum praecox Walt.
Sacciolepis striata (L.) Nash
Setaria magna Griseb.

POLYGALACEAE

Polygala cruciata Nutt.
Polygala cymosa Walt.
Polygala lutea L.

POLYGONACEAE

Polygonum opelousanum Riddell ex Small [*Polygonum hydropiperoides* Michx. var. *opelousanum* (Riddell ex Small) Stone]
Polygonum persicaria L.

RUBIACEAE

Diodia virginiana L.

SALICACEAE

Salix nigra Marsh

SAXIFRAGACEAE

Itea virginica L.

SCROPHULARIACEAE

Agalinis fasciculata (Ell.) Raf.
Agalinis linifolia (Nutt.) Britt.
Agalinis virgata Raf.

SMILACACEAE

Smilax laurifolia L.

VIOLACEAE

Viola lanceolata L.

XYRIDACEAE

Xyris ambigua Bey. ex Kunth.
Xyris caroliniana Walt.
Xyris jupicai L.
Xyris smalliana Nash

DISCUSSION

Following Schafale and Weakley (1990), limesinks in the Park can be classified as either Depression Pocosins, Small Depression Ponds, or Vernal Pools. Depression Pocosins are characterized by a dense to fairly dense shrub layer and a sparse to fairly dense tree layer. Of the limesinks surveyed, only Gum Pond with its canopy of black gum, pond cypress, and red maple fits that description. Small Depression Ponds are permanently or nearly permanently flooded in the center and may have scattered pond cypresses and black gums. Cypress Pond is an example of a small depression pond, although a portion of its east section has characteristics of a vernal pool. Vernal Pools are seasonally flooded depressions dominated by herbs, although there may be a few wetland trees or shrubs in the depression interior. In the park, vernal pools include Grass, Dry, Lily, Loblolly, and Sawgrass Ponds. In many cases, classification of limesinks is difficult when characteristics overlap two or more of these community types. According to Schafale and Weakley (1990), "Differences in hydroperiod seem to be responsible for the different vegetation of the community types. The three types may represent different stages in primary succession, which is proceeding at different rates in different depressions." Seasonal fluctuation in water levels and its variation among years appears to be an important factor in determining presence of plant species. Because the ponds have no surface exits, they hold water fairly well in wet years. The deepest ponds may have several feet of standing water; in dry years they may be completely dry. During the growing season that these limesinks were surveyed, most of the depressions had some standing water from January to April, then gradually dried and were without standing water for the remaining months, although soils in the deepest parts remained moist. The water table was reported to be several inches lower than usual in southeastern North Carolina during that year (D. M. DuMond, pers. comm.); as a result, some species such as *Eleocharis equisetoides* which had been reported previously were not encountered. It is likely that in a wet year additional species would be apparent. For example, *Utricularia purpurea* Walt., not seen in 1990, was reported to be in the Grass Pond in 1991 (J. Fowler, pers. comm.) and was observed in the Cypress Pond; the summer of 1991 was quite rainy. On the other hand, many rare species found in the

ponds would not be apparent during a rainy season because they would be under water. The limesinks were observed again in September 1991 and most were still full of standing water. Dry Pond had none, but its soil was quite moist; Loblolly Pond had shallow water covering about one-half its total area.

These limesinks are especially rich in species of special interest or concern because of rarity. The state record (with voucher citation in parentheses) is *Andropogon perangustatus* (*Sieren 4120*), which was found growing abundantly in moist parts of Gum Pond and the east section of Cypress Pond. Hitchcock (1951) indicated its habitat and range as "Bogs and moist pine woods, Florida and Mississippi." New Hanover county records include *Aristida affinis* (*Sieren 4095*), *A. purpurascens* (*Sieren 4127*), *A. virgata* (*Sieren 4136*), *Bartonia paniculata* (*Sieren 4094*), *Eragrostis refracta* (*Sieren 4105*), *Eupatorium leptophyllum* (*Sieren 4097*), *Linum floridanum* var. *floridanum* (*Sieren 4044*), *Lycopodium carolinianum* (*Sieren 4057*), *Paspalum praecox* (*Sieren 4049*), *Rhynchospora inundata* (*Sieren 4028*), and *Utricularia juncea* (*Sieren 4108*).

Fifteen species are on the Natural Heritage Program List of the Rare Plants of North Carolina (Weakley, 1990): *Agalinis linifolia* (occasional to locally abundant in all seven ponds), *A. virgata* (scattered to locally abundant in Cypress, Dry, Grass, Gum, and Sawgrass Ponds), *Aristida affinis* (occasional to frequent in Cypress, Grass, Gum, and Sawgrass Ponds), *Eleocharis equisetoides* (previously observed and photographed in Cypress Pond), *E. melanocarpa* (frequent and abundant in Loblolly Pond), *Eupatorium leptophyllum* (scattered under pond cypresses in Cypress Pond), *Lachnocaulon beyrichianum* (frequent in the woods/pond ecotones around Cypress, Dry, Grass, Gum and Loblolly Ponds), *Ludwigia linifolia* (scattered to abundant in Cypress and Grass Ponds), *L. suffruticosa* (frequent in Cypress and Sawgrass Ponds), *Panicum tenerum* (occasional in Cypress Pond), *Psilocarya scirpoides* (abundant in Lily Pond), *Rhexia cubensis* (scattered to numerous in Dry, Cypress, Grass, and Gum Ponds), *Rhynchospora pleiantha* (abundant in patches in Dry, Grass, and Cypress Ponds), *R. tracyi* (several plants in Cypress and Sawgrass Ponds), and *Scleria georgiana* (scattered in Dry and Sawgrass Ponds). An additional 13 species are on the North Carolina Watch List which includes plant species that appear to be rare or otherwise threatened with serious decline, but which have not yet been placed on

the Rare Plant List of North Carolina (Weakley, 1990). These species are *Agalinis fasciculata* (one plant in the Sawgrass Pond), *Andropogon capillipes* (scattered to abundant on the dry margins of Dry, Cypress, Loblolly, and Sawgrass Ponds and also observed in a pocosin/savannah ecotone and in other scattered depressions in the park), *Bartonia paniculata* (scattered in Cypress, Grass, and Sawgrass Ponds), *B. verna* (frequent to numerous in Grass, Gum, and Sawgrass Ponds), *Burmannia biflora* (several plants in Sawgrass Pond), *Coelorachis rugosa* (few to numerous in Gum and Sawgrass Ponds), *Ilex cassine* (occasional to numerous on the dry margins of all seven ponds), *Juncus abortivus* (scattered to locally numerous in Cypress, Dry, Grass, and Sawgrass Ponds and also observed in two pocosins in the park), *Paspalum praecox* (occasional in Sawgrass Pond), *Rhynchospora filifolia* (locally abundant in Cypress and Gum Ponds), *R. inundata* (abundant in Lily Pond, the dominant herb in mid-summer), *R. wrightiana* (locally abundant in Loblolly and Sawgrass Ponds), and *Xyris smalliana* (occasional in Grass Pond).

Cypress Pond, which has the greatest variety of habitats, also has the largest number of rare or watch list species (18), followed by Sawgrass Pond with 15, Grass Pond with 12, Dry and Gum Ponds with 8 each, Loblolly Pond with 5, and Lily Pond with 3.

Vegetation of the limesinks is clearly denser and more diverse than that of the surrounding longleaf pine–scrub oak communities. Mesic depressions have the most diversity, and it is assumed that an appropriate amount of moisture is significant in the distribution of limesink species. The presence of so many rare species in the depressions suggests that there may be a unique combination of factors responsible. Beal (1977) provided habitat data for many marsh and aquatic vascular plants of North Carolina, including eight of the rare species found in the limesinks. An analysis of Beal's data for the pH of the habitats for those eight species indicated that most were growing in sites that were neutral to alkaline. Three of the species were collected at least once in conditions which were acid (pH 4–4.9), but two of those were also collected in alkaline sites. Similarly, chloride content for most species was between 0–1 ppm, but in two cases those limits were exceeded. A study of limesinks for these and other environmental factors should provide a greater understanding of conditions controlling the distribution of limesink species.

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DEPARTMENT OF BIOLOGICAL SCIENCES
UNIVERSITY OF NORTH CAROLINA AT WILMINGTON
WILMINGTON, NC 28403

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THE NORTHEASTWARD SPREAD OF *MICROSTEGIUM VIMINEUM* (POACEAE) INTO NEW YORK AND ADJACENT STATES

DAVID M. HUNT AND ROBERT E. ZAREMBA

ABSTRACT

Microstegium vimineum is a weedy species which has recently spread from New Jersey into New York and Connecticut. It has been collected at two sites along the Hudson River in New York and reported from three sites in Connecticut. Because of its ability to invade rapidly into disturbed areas, this grass may pose a threat to rare native associate species.

Key Words: *Microstegium vimineum,* grass, weed, exotic species, geographical distribution, New Jersey, New York, Connecticut

Microstegium vimineum (Trin.) A. Camus [= *Eulalia viminea* (Trin.) Kuntze] was introduced from Asia into Tennessee about 1919 (Fairbrothers and Gray, 1972). By 1960 this grass had naturalized and spread northward to Ohio and Pennsylvania, and eastward to all the Atlantic coastal states from Florida to New Jersey. Its geographical range has steadily expanded northeastward from Tennessee, reaching Pennsylvania in 1938, Delaware in 1942 and New Jersey in 1959 (Fairbrothers and Gray, 1972).

Since the first report of this grass from New Jersey in 1959, it has increased in abundance and spread throughout the state. According to L. Mehrhoff and D. Snyder (pers. comm.), *Microstegium vimineum* was uncommon in New Jersey ten years ago, but is now widespread. Collections from two sites in northern New Jersey during 1989 are deposited at CHRB (*Hunt NJ42,* Morris Co., Jefferson Township, along Russia Brook; *Hunt NJ43,* Somerset Co., Bernards Township, along tributary of Peapack Brook). Additionally, this grass was observed between 1988 and 1990 by the senior author at seven other sites in northern and central New Jersey (Hunterdon Co.: Readington Township; Middlesex Co.: Cranbury Township; Somerset Co.: Bedminster, Warren and Bernards Townships). These observations were invariably along rivers or small tributaries, including Millstone River, Passaic River, Chambers Brook and Muddy Run.

Fairbrothers and Gray (1972) noted that *Microstegium vimineum* occupies various habitats including creek banks, river bluffs, floodplains, damp fields, swamps, lawns, woodland thickets and

roadside ditches. In New Jersey, this species was found in habitats ranging from forested, scrub-shrub and emergent wetlands to pastures, early successional fields, and forested and disturbed uplands. It was commonly observed in transitional floodplain forests dominated by *Acer rubrum* L., *Ulmus americana* L., *Impatiens capensis* Meerb. and *Onoclea sensibilis* L., in shallow emergent wetlands along small streams with *Cornus amomum* Mill., *Rosa multiflora* Thunb. and *Polygonum sagittatum* L., and in wet meadows with *Carex lurida* Wahl., *Juncus effusus* L., *Phalaris arundinacea* L. and *Euthamia graminifolia* (L.) Nutt. Barden (1987) noted that this grass readily invades and occurs most abundantly in areas which have undergone natural (e.g., flood scouring) and artificial (e.g., mowing, tilling) disturbance.

Microstegium vimineum has most recently spread northeastward from New Jersey into New York. Fertile collections made in September 1987 from two sites registered by The Nature Conservancy (TNC) in the Hudson River Valley are deposited at NYS (*Zaremba 4254*, Dutchess Co., Town of Fishkill, red maple woods near a man-made berm on the S Side of Fishkill Creek near its mouth; *Zaremba 4255*, Rockland Co., Town of Stony Point, moist open forested wetland on Round Island). These specimens may be the only collections of this species from New York since this species is absent from the recent Checklist of New York State Plants (Mitchell, 1986).

The spread of *Microstegium vimineum* has also continued northeastward into Connecticut. Populations were recently observed at a site owned by TNC in the Town of Haddam (Middlesex Co.) along the Connecticut River (L. Mehrhoff, pers. comm.), and in New Haven (New Haven Co.) and New London (New London Co.) (G. Tucker, pers. comm.). These reports may be the first of the occurrence of *M. vimineum* in Connecticut and New England, as this grass is not listed in Seymour's (1989) *Flora of New England.*

Because *Microstegium vimineum* is apparently lacking in uplands which intervene between the Hudson and Connecticut Rivers, it is hypothesized that this species may be nearing its northern limit due to a lack of cold hardiness. Barden (1987) noted the susceptibility of North Carolina populations to late frost. This species may continue to spread northeastward to a limited extent along estuaries of Connecticut, Rhode Island and southeastern

Massachusetts where the local climate is warmer than adjacent inland areas. It may also spread farther upstream to the tidal limits of the Hudson and Connecticut Rivers and their tributaries and increase in abundance in the lower Hudson and Connecticut River Valleys.

A second possible explanation for the distribution of *Microstegium vimineum* is that it occurs primarily in areas of red clay soils. New Jersey collections were from the Piedmont physiographic province, noted for such soils. This species was commonly found in alluvial soils composed of sandy clay loam associated with crimson-colored Brunswick shale. This grass is considered a characteristic Piedmont species (Godfrey, 1980) and its distribution in Georgia (Jones and Coile, 1988) and the Carolinas (Radford et al., 1968; Barden, 1987) corresponds closely with the limits of the Piedmont in these states. The New York and Connecticut populations occur in areas where red clay is locally abundant. If soil type is limiting the spread of *M. vimineum,* then this species may be approaching its maximal geographic extent in New York and New England, since large areas of red clay are uncommon outside the Hudson and Connecticut River Valleys. In this respect, *M. vimineum* may parallel other taxa whose range is closely linked to the distribution of red clay soils such as *Quercus marilandica* Muenchh., *Q. stellata* Wang., *Diospyros virginiana* L., *Pinus echinata* Mill. and *Asclepias viridiflora* Raf.

Microstegium vimineum is colonial in nature, rooting at the nodes and forming dense monotypic stands. A rapid rate of spread has been documented for this species, especially in disturbed areas (Barden, 1987). Although it may not be as aggressive and form colonies as dense and as tall as *Phragmites australis* (Cav.) Trin. ex Steud., *Lythrum salicaria* L. or other exotic species, it could threaten uncommon native wetland species along the Hudson and Connecticut Rivers. It may become necessary to establish an active monitoring and eradication program to ensure survival of these rare species. The North Carolina office of TNC is preparing an "Element Stewardship Abstract" for *M. vimineum* which summarizes the ecology of the species, the threat it poses to native vegetation, and known means of control. It is the intent of this article to increase awareness of the potential danger of this weedy species in the northeast with regard to possible future extirpation of rare native associate species.

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NEW YORK FIELD OFFICE
THE NATURE CONSERVANCY
1736 WESTERN AVE.
ALBANY, NY 12203

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NATURAL PLANT COMMUNITIES OF BERKSHIRE COUNTY, MASSACHUSETTS[1]

PAMELA B. WEATHERBEE AND GARRETT E. CROW

ABSTRACT

The natural plant communities and habitats of Berkshire County, Massachusetts, are described. Communities are delineated by a description of the physical characteristics of the habitat and typical vegetation. An extensive list of species most closely associated with each community is provided. Distribution of the communities within the county is discussed, and examples are given. Other factors, both biotic and abiotic, that influence development of each community are noted.

Key Words: Natural plant communities, habitats, Berkshire County, Massachusetts

INTRODUCTION

Berkshire County covers 260,860 ha and is located at the western end of Massachusetts. Varied topography and bedrock have resulted in diverse habitats that support a flora of 1777 taxa (Weatherbee, 1990), both native and introduced, including 117 state-listed rare taxa (Sorrie, 1989; they are indicated by an asterisk in this discussion).

The plant communities described below for Berkshire County are based in large part on Rawinski's (1983) outline of a classification of natural communities in New England. In his classification, the communities are described by a brief description of physical characteristics of the habitat and physiognomy of the community, and are identified by a few of the most characteristic plant and animal species. Although less detailed, his descriptions of communities are similar in scope to that of Reschke (1980) for adjacent New York State, but we found Rawinski's classification more applicable to New England.

For this study, information on species composition was derived from extensive field notes of the senior author made during the preparation of a Flora of Berkshire County (Weatherbee, 1990), from notes made by Bruce Sorrie, former Massachusetts Natural Heritage and Endangered Species Program Botanist, and from theses and published studies conducted in Berkshire County. Us-

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ing this information, the authors were able to provide a much more detailed account of the vascular plant species that are characteristic of each community than that given by Rawinski (1983), and to describe the structure of those communities in Berkshire County.

The most important factors determining habitat and plant community relate to bedrock geology (Figure 1) and to the impact of glaciation, climate, and plant migration. Geologic events have influenced the development of soil, topographic relief, drainage patterns, and elevation (Figure 2). Bedrock described as calcareous includes the Stockbridge Formation, which consists of various types of marble, and the Walloomsac Formation which consists of calcitic and schistose marble (Zen, 1983). Regional climate determines the overall type of vegetation, but there is some variation in climate within the county due to elevational variation (176 m to 1064 m) and microclimatological differences produced by local topographical diversity. Post-glacial migration of species from various refugia south of the glacial margin or from the exposed coastal plain has played an important role in determining the pool of species which ultimately colonized available habitats and developed our plant communities.

The following 35 natural plant communities are recognized by us for Berkshire County:

Forests and Woodlands

Mesic Northern Conifer Forest
Mesic Northern Hardwood Forest
Rich Mesic Forest
Mesic Acidic Oak/Conifer Forest
Dry Acidic Oak/Conifer Forest
Dry Calcareous Oak/Conifer Forest
Floodplain Forest
Pitch Pine/Scrub Oak Barrens

Rocky Summit and Cliff Communities

Southern Acidic Rocky Summit
Southern Calcareous Rocky Summit
Southern Acidic Cliff
Southern Calcareous Cliff
Serpentine Outcrop

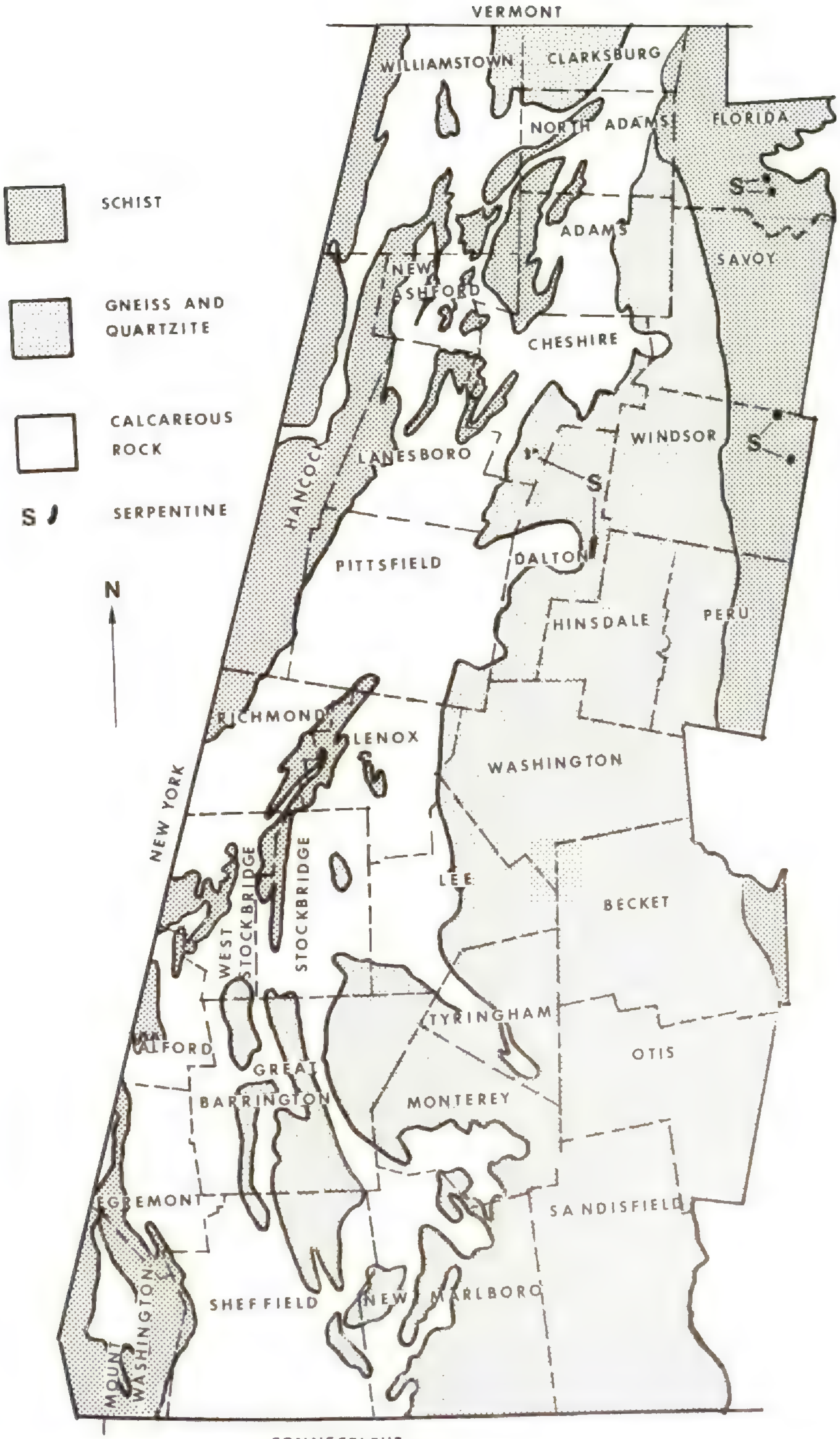

Figure 1. Bedrock geologic map of Berkshire County (redrawn from Zen, 1983).

Figure 2. Topography and physiographic regions of Berkshire County (adapted from Technical Planning Associates, 1959).

Lakes and Ponds

Clear Softwater Lake/Pond
Acidic Brownwater Lake/Pond
Moderately Alkaline Lake/Pond
Highly Alkaline Lake/Pond

Rivers, Streams and Springs

High Gradient Stream
Medium Gradient Stream
Low Gradient Stream
Spring and Spring Run

Wetlands

Acidic Conifer Swamp
Acidic Hardwood Swamp
Circumneutral Hardwood Swamp
Acidic Shrub Swamp
Circumneutral Shrub Swamp
Robust Emergent Marsh
Acidic Graminoid Marsh
Circumneutral Graminoid Marsh
Level Bog
Forested Fen
Shrub Fen
Sloping Graminoid Fen
Lake Basin Graminoid Fen
Calcareous Seep

FORESTS AND WOODLANDS

Mesic Northern Conifer Forest Community

The montane spruce-fir forest (Oosting and Billings, 1951; Cogbill, 1987), the boreal forest (Siccama, 1974) or the Northeastern Spruce-Fir Forest of Küchler (1964) are alternate terms for this community dominated by *Picea rubens* and *Abies balsamea.* It is best developed above 914 m on Mt. Greylock summit and along the adjacent ridge of Saddle Ball where these two species occur with *Betula cordifolia* and *B. alleghaniensis.* The summit,

although drastically altered now, was described in 1799 as being densely covered with stunted *Abies balsamea* (Dwight, 1822). Other associated species are *Sorbus americana, S. decora**, *Luzula parviflora* ssp. *melanocarpa**, *Amelanchier bartramiana**, *Gaultheria hispidula, Solidago macrophylla**, *Viburnum lantanoides, Ribes glandulosum, Oxalis acetosella, Cornus canadensis, Dryopteris intermedia, D. campyloptera* and *Lycopodium lucidulum.*

Many needle-leaved evergreen trees are well adapted to high elevations where a shorter frost-free season, colder average temperatures, high winds, heavy snow, lower light level and formation of rime ice due to frequent cloud cover, and shallow soil create difficult growing conditions (Marchand, 1987). In the spruce-fir zone of the Green Mountains, Siccama (1974) noted that the number of frost-free days was 93. He suggested that the elevational limit of low-hanging clouds corresponds to the elevation of the transition zone between the montane boreal forest and the northern hardwoods zone. *Abies balsamea* trees on the summit of Mt. Greylock exhibit a "table tree" form, as described by Marchand (1987). Ice particles, wind-driven over the surface of the snow, remove foliage above the snow while branches below the snow remain luxuriant.

Mesic Northern Hardwood Forest Community

This widespread community covers the slopes and summits of all but the highest mountains and also the low hills and valley sides of the northern half of the county. Within the broader boundary of this community, other communities occur locally on edaphically, topographically or climatically distinct areas. The upper elevational limit of this forest ranges from 800–850 m, which closely agrees with Siccama's (1974) estimate for this community type in northern Vermont of 792 m. Towards the southern part of the county, particularly in the valley region, this forest type grades into the Mesic Acidic Oak/Conifer Forest.

The co-dominant tree species *Acer saccharum, Fagus grandifolia* and *Betula alleghaniensis* occur in varying proportions throughout the community, with *B. alleghaniensis* becoming dominant at higher altitudes. Other trees that commonly occur are *Fraxinus americana, Betula lenta, B. papyrifera, Quercus ru-*

bra, Prunus serotina and *Acer rubrum.* Except for *Fraxinus americana,* these species may indicate a past history of disturbance, both natural and human. *Quercus rubra,* although often an important component of the mature forest, does not regenerate well in shade. Very large individuals of *Q. rubra* have been observed on some slopes of Mt. Greylock, but the regeneration around the trees is all *Acer saccharum. Tsuga canadensis* is seen in small patches in moist ravines with thin soils, steep rocky, north-facing slopes and along moist streambanks. The Mesic Northern Hardwood Forest becomes more common on the Berkshire Plateau; there it becomes intermixed with *Picea rubens* and *Abies balsamea.*

- *Acer pensylvanicum, A. spicatum, Ostrya virginiana,* and *Hamamelis virginiana,* which are adapted to growing under the closed canopy, form a characteristic understory layer. Typical shrubs include *Taxus canadensis, Viburnum lantanoides, V. acerifolium, Sambucus pubens* and *Lonicera canadensis.* The vernal flora is somewhat sparse, but *Claytonia caroliniana, Erythronium americanum, Viola rotundifolium* and *Trillium erectum* are common in the community. The ground cover includes *Lycopodium* spp., *Mitchella repens, Aster acuminatus, A. divaricatus* and the ferns *Dryopteris intermedia* and *Polystichum acrostichoides.*

Factors that influence the extent of this forest are climate and soil. Siccama (1974) found the frost-free season in the Green Mountain northern hardwoods forest to average about 144 days, 51 days longer than in the montane boreal forest. Generally the soil is well-drained, but moist throughout the year, and most often derived from a bedrock of schist (Figure 1), and less often from gneiss or quartzite. In studies of the forests of New Hampshire, Leak (1978) found typical northern hardwoods occurred on fine glacial till. Kudish (1979) indicated that *Acer saccharum* and other deciduous trees need at least a 30–90 cm layer of till to grow well, while conifers can survive on only 8–15 cm of till. His studies in the Catskills showed that till depth was more limiting than pH or elevation. This factor appears to be important in the distribution of this forest community in Berkshire County. High elevation (Siccama, 1974) with its concomitant cloud cover and shorter growing season seems to be the most important factor in limiting development of this community type on mountain slopes. Drier soils may account for the community's decreasing abundance in the southern section of the county.

Rich Mesic Forest Community

Occurring in smaller, discontinuous areas throughout the county and typically surrounded by other forest community types, sites of the Rich Mesic Forest correlate with, and are influenced by, calcareous bedrock (Figure 1) and associated alkaline groundwater. The best examples of this community are situated on slopes below calcareous outcrops, on talus below these outcrops or on fairly level sites where bedrock is near the surface. These sites tend to be on the low hills edging valleys, but they also occur higher (822 m) on the slopes of Mt. Graylock.

The community is distinguished by a dominance of *Acer saccharum* in most examples, sometimes to the near exclusion of other tree species. Other trees, in order of decreasing closeness of association with the community, are *Fraxinus americana, Tilia americana, Carya cordiformis, Betula lenta, B. alleghaniensis* and *Fagus grandifolia.* Leak (1978) found that in the White Mountains of New Hampshire, *Acer saccharum* became dominant only on enriched sites, and that *Fraxinus americana* was abundant only on these sites. Individuals of *Quercus rubra* may attain large stature and remain part of this community for a long time, but the species does not regenerate well. *Dirca palustris,* a shrub, is restricted to this habitat, and is thus an important indicator species. Additionally, *Ostrya virginiana,* an understory tree, is abundant in these rich sites.

In the Rich Mesic Forest the herbaceous species are abundant and diverse, and the community has an especially rich vernal flora. Table 1 lists these species in approximate order of decreasing degree of association with the community.

The most important determining factors in this community are the presence of calcareous rock and adequate moisture. The soil is derived from the soft, easily weathered rock. The higher pH of the soil facilitates microbial activity and decomposition of litter. Leaves of *Acer saccharum* are rich in bases (Dickinson and Pugh, 1974), thus favoring rapid decomposition and recycling of nutrients. An adequate supply of moisture is also crucial to this process and to development of mull soils typical of this community (Bormann and Buell, 1964). The litter layer is thinner than that of Northern Hardwood Forest because of rapid turnover, thus enabling the small vernal species to receive enough sunlight to emerge

Table 1. Herbs of the Rich Mesic Forest, listed in approximate order of decreasing degree of association with the community. * = State-listed rare species.

Caulophyllum thalictroides (L.) Michx.
Adiantum pedatum L. var. *pedatum*
Hepatica acutiloba DC.
Allium tricoccum Ait.
Asarum canadense L. var. *canadense*
Dentaria diphylla Michx.
Dentaria laciniata Muhl. ex Willd.
Dicentra canadensis (Goldie) Walp.
Dicentra cucullaria (L.) Bernh.
Uvularia grandiflora Sm.
Dryopteris goldiana (Hook. ex Goldie) Gray
Diplazium pycnocarpon (Spreng) Brown
Hydrophyllum virginianum L.
Carex plantaginea Lam.
**Carex hitchcockiana* Dewey
Viola rostrata Pursh
Viola selkirkii Pursh ex Goldie
Galearis spectabilis (L.) Raf.
Cypripedium calceolus L. var. *pubescens* (Willd.) Correll
**Milium effusum* L.
**Blephilia hirsuta* (Pursh) Benth. var. *hirsuta*
**Panax quinquefolius* L.
Oryzopsis racemosa (Sm.) Ricker
Hystrix patula Moench var. *patula*
Carex deweyana Schwein. var. *deweyana*
Carex amphibola Steud. var. *rigida* (Bailey) Fern.
Carex rosea Schkuhr ex Willd.
Sanicula trifoliata Bickn.
**Sanicula gregaria* Bickn.
**Waldsteinia fragarioides* (Michx.) Tratt.
Thalictrum dioicum L.
Thalictrum (*Anemonella*) *thalictroides* (L.) Eames & Boivin
Ranunculus abortivus L.
**Hydrophyllum canadense* L.
Botrychium virginianum (L.) Sw.
Viola canadensis L.
Solidago flexicaulis L.
Carex hirtifolia Mackenzie
Sanguinaria canadensis L.
Actaea pachypoda Ell.
Actaea rubra (Ait.) Willd.
Laportea canadensis L.
Osmorhiza claytonii (Michx.) Clarke

early enough in the spring to complete their life cycles before the canopy leafs out.

Mesic Acidic Oak/Conifer Forest Community

This community is found in the southern half of the county and the southern third of the Berkshire Plateau (Egler, 1940) usually in rocky, acidic soil. This community is more difficult to define. It grades into the Mesic Northern Hardwood and Dry Acidic Oak/Conifer Forests, and in some areas may represent a stage rebounding from earlier disturbance (McVaugh, 1958). Küchler's (1964) designation of this area as transitional between Mesic Northern Hardwood and Appalachian Oak, indicates the variability of this community. Westveld et al. (1956) used the term Transition Hardwoods to indicate the overlap of northern hardwoods with oaks and hickories.

Quercus rubra, Acer rubrum and *Pinus strobus* share dominance, but *Tsuga canadensis* and *Fagus grandifolia* are important, and may become more dominant as the forest matures, as Egler (1940) describes for the southern section of the Berkshire Plateau. *Prunus serotina, Betula lenta* and *B. papyrifera* are common. Understory trees and shrubs include *Acer pensylvanicum, Kalmia latifolia, Amelanchier arborea, Hamamelis virginiana,* and *Viburnum acerifolium.* The ground cover layer is often somewhat sparse, but typical species include *Lycopodium obscurum, Polystichum acrostichoides, Medeola virginiana, Maianthemum canadense, Aster divaricatus, Polygonum cilinode, Aralia nudicaulis,* and *Carex pensylvanica.* Soil derived from acidic bedrock, such as quartzite or gneiss (Figure 1), tends to be rocky, shallow, well-drained and poor in nutrients. These soil characteristics seem to be important in the distribution of this community. Kudish (1979) states that the tree species characteristic of this community can subsist on minimum till depths of 20–45 cm. Leaves of *Quercus rubra* do not decompose quickly, resulting in the development of a thick litter layer; they also contribute to the development of acidic soil. The same is true of the needles of *Pinus strobus* and *Tsuga canadensis* (Dickinson and Pugh, 1974). Acidic, shallow soil is not favorable for growth of *Acer saccharum,* thus this species is often absent. *Betula alleghaniensis* is often scarce as well. Since the canopy of *Quercus rubra* is more open than a canopy of *Acer saccharum,* the light levels that reach the forest

floor favor reproduction of *Quercus rubra* and *Acer rubrum,* species that require higher light levels for seedling growth.

Dry Acidic Oak/Conifer Forest Community

This community, dominated by species of *Quercus,* occurs on soils derived from acidic rock, typically from quartzite (Figure 1), on upper slopes where the soil is thin and excessively well-drained. Sites occur throughout the Berkshires, particularly on south-facing slopes, but the community is more common in the southern half of the county.

Quercus prinus, along with *Q. velutina, Q. alba* and *Pinus rigida,* are the typical tree species, but *Pinus strobus, Betula papyrifera, Acer rubrum* and *B. lenta* are also very common. *Castanea dentata* is frequently present, and may attain small tree size before succumbing to Chestnut blight. *Carya glabra* occurs most commonly in southernmost towns, and *Sassafras albidum* may be locally common. The canopy is quite open, and ericaceous shrubs, such as *Vaccinium angustifolium, V. pallida, Gaylussacia baccata, Rhododendron prinophyllum* and *Kalmia angustifolia* form a dense shrub layer. *Gaultheria procumbens* and *Epigaea repens* are common evergreen ground cover species in more open areas. Herbaceous species are few and are represented by *Pteridium aquilinum, Melampyrum lineare, Cypripedium acaule, Lysimachia quadrifolia* and, uncommonly, *Isotria verticillata.*

The thin, dry soil that develops over acidic bedrock with many fractures and joints providing drainage, is an important factor in the distribution of this community. Because decomposition of litter and development of soil is slow in acidic sites (Dickinson and Pugh, 1974), these soils tend to be thin and infertile (McIntosh, 1959). The openness of the forest canopy, coupled with an often south-facing slope, allows high insolation of the soil, which results in increased dryness and higher soil temperatures (Cantlon, 1953). Succession to a more mesic and closed-canopy forest may occur (Little, 1973), but this process may easily be set back by the occurrence of an occasional fire, to which this community is particularly susceptible. Fire, which reduces ground cover and stimulates the opening of serotinous cones (Elias, 1987), is important to the regeneration of *Pinus rigida.* This community shares many species with, and gradually grades into, the Southern

Acidic Rocky Summit Community, a community that usually occupies the ridges above this community.

Dry Calcareous Oak/Conifer Forest Community

This community, occupying well-drained slopes or low ridges underlain with calcareous rock (Figure 1), occurs more commonly in the southern half of the county. In the north, it is found occasionally on south- or southwest-facing slopes, but lacks some of the characteristic species of the community type as it occurs in the southernmost towns. These more southerly species are designated by a plus sign (+) in the following discussion.

Quercus alba, Q. velutina and *Q. muhlenbergii**+ are characteristic of this community, along with *Carya ovata* and *Ostrya virginiana. Pinus strobus* and *Quercus rubra* occur commonly, although scattered. The understory trees *Cornus florida* and *Staphylea trifolia*+, flourish under this more open canopy. *Carya ovata* and *Ostrya virginiana* often form a distinct association, with which two rare grasses occur: *Poa languida** and *Sphenopholis nitida**. The community is rich in herbaceous species, which are listed in Table 2 in approximate order of decreasing degree of association with the community.

Bedrock, slope and aspect play an important part in the composition of this community. The soil, a fine sandy or clayey loam, is strongly influenced by the calcareous bedrock, which may be near the soil surface, or may occur as an outcrop. In contrast to the Rich Mesic Forest, there is no seepage of groundwater. A topographical barrier, a ridge of 426 m elevation, rises north of Lanesborough, and may have prevented those species common in the southern part of the county from spreading to northern sites, in addition, there is little suitable habitat. The high number of herbaceous species may relate to the less dense *Quercus* spp. canopy and high soil fertility derived from calcareous bedrock.

Floodplain Forest Community

This well-defined community occurs on deep, alluvial soil bordering the low-gradient sections of the major rivers: the Housatonic, Hoosic, Green (in Great Barrington), Williams, Konkapot and Deerfield Rivers. The community which experiences periodic flooding, most frequently in the spring, may occur as a narrow

Table 2. Herbs of the Dry Calcareous Oak/Conifer Forest, listed in approximate order of decreasing degree of association with the community. + = Species restricted to southern-most towns. * = State-listed rare species.

Asclepias quadrifolia Jacq.
Arabis canadensis L.
+*Lespedeza violacea* (L.) Pers.
Lespedeza intermedia (S. Wats.) Britt.
Rosa carolina L.
Aureolaria flava (L.) Farw.
+*Aureolaria virginica* (L.) Pennell
Linum virginianum L.
+*Ranunculus hispidus* Michx. var. *hispidus*
+**Chamaelirium luteum* (L.) Gray
+*Muhlenbergia tenuiflora* (Willd.) BSP.
+*Silene caroliniana* Walt. var. *pensylvanica* (Michx.) Fern.
+*Paronychia canadensis* (L.) Wood
+*Desmodium rotundifolium* DC.
Hieracium venosum var. *nudicaule* (Michx.) Farw.
**Sphenopholis nitida* (Biehl.) Scribn.
**Poa languida* Hitchc.
+*Helianthus divaricatus* L.
Carex eburnea Boott
+*Viola triloba* Schwein. var. *dilatata* (Ell.) Brainerd
Campanula rotundifolia L.
Triosteum aurantiacum Bickn.
Hepatica americana (DC.) Ker.
Ceanothus americanus L.
Desmodium nudiflorum (L.) DC.
Desmodium paniculatum (L.) DC. var. *paniculatum*
Uvularia perfoliata L.

band along the river or as extensive flat areas, and include oxbow ponds and associated marshes. In some areas there is a step-wise series of terraces back from the river, the highest level being the driest. Silt bars and mud banks provide small pioneer habitats, colonized by a few annual species or by seedlings of the Floodplain Forest trees. Many of these rich alluvial habitats have been cleared for agriculture, leaving only a narrow strip, if any, of the original vegetation along the river.

Salix nigra, Platanus occidentalis and *Populus deltoides* are early colonizers of banks and silt bars (Nichols, 1916) and are more often found nearest the river. *Acer negundo* is more common as a floodplain tree along the Hoosic River, while *A. saccharinum* is dominant on floodplains in the Housatonic River watershed. *Acer nigrum** is locally common. *Ulmus americana,* formerly

common along floodplains, is now more typically represented by bare, dead trunks than by living trees. *Fraxinus pennsylvanica* is usually found on riverbanks, while *Juglans cinerea, Tilia americana* and *Celtis occidentalis* typically occupy the upper alluvial terraces of the floodplain.

There are few shrubs characteristic of the floodplain; however, introduced *Lonicera morrowii* has become weedy. Several woody vines, *Vitis riparia, Parthenocissus quinquefolia* and *Menispermum canadense,* and the herbaceous vines, *Echinocystis lobata* and *Sicyos angulatus,* flourish on the floodplains.

Many of the herbaceous species (Table 3) occur restricted to floodplain forests or are more commonly associated with this community.

Inundation is the major factor influencing in development of this community. Plants growing in a typical floodplain, which is usually inundated for a significant length of time only during the spring (Nichols, 1916), must be adapted to withstand a reduced oxygen supply to their roots during that time. Likewise, these species must tolerate a high water table most of the year. The impact of inundation may account for the lack of a shrub layer. Ice floes scour banks and silt bars, resulting in many newly disturbed sites, open for colonization. The cutting of a new channel may shift the river, resulting in somewhat isolated floodplain remnants. The environment of a river is one of constant change.

The soil, silt that has been deposited by the river, is typically deep, without distinct horizons and contains considerable organic matter (Rawinski, 1983). The woody species occupying these sites typically grow to a large size, and herbaceous growth can likewise be exceedingly vigorous and tall. Calcareous rock underlies portions of these river valleys, and probably influences the higher fertility of the soil.

Pitch Pine/Scrub Oak Barren Community

This community once occurred extensively on the sandy outwash plains along the Housatonic and Konkapot Rivers in the southernmost towns of Sheffield and New Marlborough. *Pinus rigida* and *Quercus ilicifolia* dominated an open woodland with a dense shrub layer of *Vaccinium angustifolium, V. pallidum* and *Gaylussacia baccata.* Grassy clearings were dominated by *Schizachyrium* (*Andropogon*) *scoparium,* and *Quercus prinoides* oc-

Table 3. Herbs of the Floodplain Forest, listed in approximate order of decreasing degree of association with the community. * = State-listed rare species.

**Arisaema dracontium* (L.) Schott
**Carex davisii* Schwein. & Torr.
**Carex grayi* Carey
**Carex trichocarpa* Schkuhr
**Carex tuckermanii* Dewey
**Carex typhina* Michx.
Polygonatum biflorum (Walt.) Ell. var. *commutatum* (Schultes f.) Morong
Allium canadense L. var. *canadense*
Xanthium strumarium L. var. *canadense* (P. Mill.) Torr. & Gray
Ambrosia trifida L.
Helenium autumnale L. var. *autumnale*
Teucrium canadense L. var. *virginicum* (L.) Eat.
Ribes americanum Mill.
Urtica dioica L. ssp. *dioica*
**Claytonia virginiana* L.
**Carex alopecoidea* Tuckerm.
Rudbeckia laciniata L.
**Aster prenanthoides* Muhl.
Elymus wiegandii Fern.
Elymus riparius Wieg.
**Elymus villosus* Muhl. ex Willd.
Bromus altissimus Pursh
Matteuccia struthiopteris (L.) Todaro
Carex hirtifolia Mackenzie
Geum laciniatum Murr. var. *trichocarpum* Fern.
Scrophularia marilandica L.
Rorippa palustris (L.) Bess. var. *fernaldiana* (Butters & Abbe) Stuckey
Carex spregnelii Dewey ex Spreng.

curred as scattered shrubs along with the herbaceous species characteristic of this habitat.

At present, agriculture and residential housing fragment these natural habitats. While formerly dominant, *Pinus rigida* now is being displaced by *Pinus strobus, Quercus alba, Q. rubra, Q. coccinea, Acer rubrum* and *Prunus serotina. Quercus ilicifolia* now occurs primarily on roadsides and edges of this successional forest. *Vaccinium angustifolia, V. pallida* and *Gaylussacia baccata* persist as the shrub layer, along with species more commonly found in Mesic or Dry Acidic Oak/Conifer Forest. The following species typical of grassy clearings are now found along roadsides or in clearcuts in the sandplain area: *Quercus prinoides, Carex brevior, Dichanthelium oligosanthes, Schizachyrium* (*Andropogon*) *sco-*

parium, Cyperus filiculmis, Bulbostylis capillaris, Juncus secundus, Rhus copallina, Helianthemum canadense, Hypericum gentianoides, Linaria canadensis, Aster linariifolius and *Krigia virginica.* Species that were listed by Hoffmann (1922) as occasional or common on the sandplain, but have not been re-located since in Berkshire County, include *Helianthemum bicknellii, Lupinus perennis, Crotalaria sagittalis, Asclepias amplexicaulis* and *A. tuberosa.*

These communities are strongly influenced by dry, sandy soil, and are fire dependent. Breakdown of litter is slow because of dryness and low pH of the soil, which results in considerable accumulation of litter, a condition conducive to fire. Fire removes litter, creating conditions that allow sunlight to reach the soil (Henderson, 1982). Bare mineral soil is often necessary for the regeneration of species adapted to fire, such as *Pinus rigida.* However, due to development, incidents of fire are suppressed so that it is unlikely to be a factor in the future. The absence of burning allows conditions conducive to a vegetational change favoring establishment of *Quercus* spp., other hardwoods, and *Pinus strobus,* as noted by Seischab and Bernard (1991) in New York State.

ROCKY SUMMIT AND CLIFF COMMUNITIES

Localities occupied by rocky summit and cliff communities are limited in extent, as exposed rock is rare in this generally mesic region. Acidic bedrock, either gneiss, schist or quartzite, most often is found on summits and ridgetops. In calcareous regions the rock is easily weathered, resulting in few distinct outcrops or vertical cliffs, especially at higher elevations. Differences between the summit and cliff communities may be difficult to define as ridgetops quickly grade into more shaded lower slopes and ledges.

Southern Acidic Rocky Summit Community

Occupying mountain summits and ridges, this community is more common on the southern Taconic summits of the elevation range from 600–792 m, notably Mt. Everett, Mt. Race and Alander Mountain in the southwest portion of the county, on East (533 m) and Monument Mountains (533 m) and on Pine Cobble Mountain (560 m) in the north.

Vegetationally, this community is closely related to the Dry

Acidic Oak/Conifer Forest, but is characterized by larger areas of open bedrock, scattered small trees and dense low shrub growth. *Pinus rigida* is always present, and on the southern Taconic ridges growth of *Quercus ilicifolia* may be very dense. Other trees, such as *Betula papyrifera, Quercus rubra* and *Acer rubrum,* may appear in a rather stunted form. *Juniperus communis* occurs occasionally. The shrub layer is a dense growth of ericaceous shrubs including *Vaccinium angustifolium, Gaylussacia baccata* and *Rhododendron prinophyllum.* On a few southern summits, *Arctostaphylos uva-ursi* occurs in open sunny areas at the edges of outcrops. Other shrubs that grow mixed with these species are *Aronia melanocarpa, Amelanchier stolonifera* and, uncommonly, *Prunus pumila* var. *susquehanae. Potentilla tridentata* appears frequently in openings, as it does on more northern, higher, open ridges.

Diversity of herbaceous species is low: *Woodsia ilvensis* occurs occasionally in southern locations; *Deschampsia flexuosa* and *Schizachyrium scoparium* are common tuft-forming grass species; *Carex pensylvanica* forms extensive patches; *Corydalis sempervirens* is frequent in shallow soil pockets on open rock.

Physiognomy of this community is usually one of extensive low shrubs with few trees. However, an unusual dwarf "forest" of *Pinus rigida,* with *Quercus ilicifolia,* is found on the flat summit of Mt. Everett and on a level ridge in Clarksburg on the southern extension of the Green Mountains; *Quercus ilicifolia* is not present in the latter site. The dwarf trees average about 1 m in height, and present a flat-topped, laterally-growing aspect. Keith (1912) quotes Professor Edward Hitchcock's description of Mt. Everett's summit in 1839: "a naked eminence with numerous yellow pines, two or three feet high." McIntosh (1959) notes a similar dwarf *Pinus rigida* forest on a flat-topped summit in the Shawangunk Mountains of New York.

These summits, unlike most others in the county, have thin soil overlying the schist or quartzite, and what little organic material is there accumulates slowly. There is slight inflow of nutrients, such as might occur on a slope. Conditions are quite xeric, and the lack of a tree canopy allows extremes of heat and dryness to occur. Wind is probably not an important factor in keeping the vegetation low, as there are many higher ridges that are occupied by taller forests; however, fire may be a factor. McVaugh (1958) commented on the possible succession of this community and concluded that it appeared stable. Hoffman (1922) observed

the same species that are presently seen, particularly an *Arctostaphylos uva-ursi* population which was known to Dewey (*in* Field, 1829). Areas dominated by *Vaccinium angustifolium* exist on some northern mountain ridges, but these appear to be abandoned pastures that were colonized by *V. angustifolium.* At one time, these areas were burned to maintain the blueberry fields, but they are now being slowly invaded by forest.

Southern Calcareous Rocky Summit Community

Rare throughout the county, usually this community occurs on ridgetops of low hills edging the main valleys, but there are a few high ridges whose rocks, while not true limestone or marble, have a distinct calcareous influence. West Stockbridge and Tom Ball Mountains are good examples.

These open, dry rock outcrops support a vegetation whose species are intolerant of much shade, and require calcareous soil. Many of the plants that are specific for these situations are adapted to growing in crevices with little soil, *Carex eburnea* will often be abundant in such sites. *Clematis occidentalis** is frequent at these sites, while *Trichostema* (*Isanthus*) *brachiatum**, *Minuartia michauxii** and *Lonicera hirsuta** are rare. More northerly elements, rare *Rosa acicularis** growing with *Senecio pauperculus,* occupy a high ridge (532 m) in the northern third of the county. Tom Ball and West Stockbridge Mountains, sharp north-south trending ridges, support a mixture of both lime- and acid-loving species. *Hedyotis longifolia** and *Arabis lyrata** grow with *Woodsia ilvensis,* an acidophile, in crevices on open rock. *Amelanchier sanguinea** forms small patches close to *Gaylussacia baccata, Pinus rigida,* and *Potentilla tridentata. Pinus resinosa,* a native species in Berkshire County, occurs only on these ridges. *Viburnum rafinesquianum** tends to grow in more shaded situations on summits and also on rocky south-facing slopes.

The tendency of trees to uproot and pull away from the steep-sided outcrops maintains the open aspect. Rocks splitting off from sharp ridges also renew open areas, and dry, shallow soil discourages woody growth.

Southern Acidic Cliff Community

Suitable habitat for the establishment of this community is widespread. The vegetation is sparse, and not chacterized by a

specific or distinctive group of plants, unlike the Southern Calcareous Cliff Community. *Polypodium virginianum* is always present in crevices and forms large mats on boulders, along with *Aralia hispida, Dryopteris marginalis, Polygonum cilinode, Diervilla lonicera* and *Parthenocissus quinquefolia,* all plants found commonly in acidic situations. Two of the few rare plants found in this habitat are *Asplenium montanum**, which occurs in two localities on quartzite, and *Adlumia fungosa**, found on boulder talus below cliffs.

This habitat is cooler, moister and more shaded than the Summit Community. The acidic rock produces little soil and nutrients for vegetation, and when shaded becomes unfavorable for many species.

Southern Calcareous Cliff Community

This uncommon community is found on steep cliff faces or sloping rock outcrops. Frequently, the ridge is capped with resistant rock while the soft limestone beneath has eroded into ledges and outcrops. The habitat, while found throughout the western part of the county, is best represented in Sheffield, particularly on Bartholomew's Cobble. The vegetation, which includes many of the county's rarer species, is distinct and specific to the habitat. The small ferns, *Pellaea atropurpurea, Asplenium ruta-muraria**, *A. trichomanes, A. platyneuron* and *Woodsia obtusa* colonize sunny or slightly shaded crevices, *Asplenium rhizophyllum* occurs on moss-covered rock faces, while *Selaginella rupestris* and *Campanula rotundifolia* prefer dry, shallow soil pockets on open rock. *Parietaria pensylvanica* colonizes dry to moist rock outcrops; *Arabis lyrata**, *A. laevigata**, *A. hirsuta* and *Saxifraga virginiensis* colonize shaded, moist, deeper pockets of soil, and *Cystopteris bulbifera* and *C. tenuis* are common on moist, shaded calcareous rock. Of the few northern elements, *Cryptogramma stelleri** is found on dripping cliffs and *Woodsia glabella** inhabits shaded crevices in a high, northern cliff.

Few trees or shrubs can grow on these steep rock faces, therefore there is sufficient light and sites for the small species that are adapted for survival on little soil. This diverse community of plants is in contrast to the species poor, sparse vegetation of the Acidic Cliff Community sites.

Serpentine Outcrop Community

There are five or six locations for ultramafic rock in the northeastern part of the county (Figure 1), only two of which occur as exposed outcrops. This bedrock is part of a narrow belt of serpentine rock occurrences along the east flank of the Appalachian Mountains that extends from Alabama to Newfoundland (Zika and Dann, 1985). Serpentine is found as intrusive rock in quartzite, gniess and schist on the Berkshire Plateau.

The sharp contrast between vegetation of serpentine and non-serpentine soils is well-documented (Walker, 1954). This community of serpentine outcrops is characterized as open, with sparse and stunted vegetation, and by the presence of serpentine species, which typically have disjunct distributions, or are even endemic (Zika and Dann, 1985). The outcrops in the county are not large enough to support an extensive serpentine vegetation. *Moehringia macrophylla** is the only taxon on these outcrops that is restricted to serpentine outcrops. *Cerastium arvense* is most abundant on serpentine outcrops, but is also found occasionally in open rocky woods. Other taxa frequent on these serpentine formations include *Asplenium trichomanes* and *Campanula rotundifolia.* The most extensive outcrop, in the town of Florida, also supports other taxa that are considered somewhat calciphilic, such as *Selaginella rupestris* and *Aquilegia canadensis.* In other areas where the slope is not steep, soil may overlie the ultramafic rock, and the vegetation is not notably distinct.

Infertility of serpentine soils is the result of complex factors, and plants endemic to serpentine have developed a variety of adaptations to these conditions. Serpentine rock and its derived soils are high in magnesium, iron and the heavy metals chromium and nickel, but usually deficient in major nutrients such as calcium, nitrogen and phosphorus (Walker, 1954; Brooks, 1987). Lack of organic matter and droughty characteristics of the soil contribute to infertility.

LAKES AND PONDS

These aquatic habitats are classified according to the alkalinity of the water, the most important factor influencing the distribution of species. Hellquist (1980), in his study of the distribution of *Potamogeton* in New England, classified them into six groups,

and found that the occurrence of most *Potamogeton* species was strongly correlated with certain ranges of alkalinity. Some species are restricted to a narrow range, but others many tolerate a wide range (Hellquist, 1980). Other aquatics likewise have distributions that correlate with alkalinity of the waters, which is affected by its origin in either acidic or calcareous bedrock. Alkalinity ranges of many aquatics are given in a series of papers on aquatic plants of New England (Crow and Hellquist, 1981, 1982, 1983, 1985; Hellquist and Crow, 1980, 1981, 1982, 1984). Depth of water, bottom conditions, water clarity, velocity of flow and habitat elevation are also important factors that determine species composition of an aquatic habitat.

Clear Softwater Lake/Pond Community

Water bodies with extremely acidic waters occur in regions of acidic bedrock, usually schist or gneiss, at elevations between 448 and 622 m. Most acidic waters occur on the Berkshire Plateau where the poorly-drained, rolling topography has resulted in creation of many lakes and ponds; a few occur on the uplands of the Taconic Range.

Vegetation in general is characterized by submersed species with a rosette growth form and *Potamogeton* spp. that are restricted to very acidic waters. *Isoetes echinospora, Eriocaulon pellucidum* (= *E. septangulare*), *Sagittaria graminea, Elatine minima* and *Lobelia dortmanna* all have a submersed rosette of leaves. *Potamogeton confervoides, P. bicupulatus* and *P. oakesianus* are found only in these extremely acidic waters (Hellquist, 1980). *Potamogeton spirillus* occurs, but is not restricted to the most acidic waters. Floating-leaved components of this community are the common and widespread *Nuphar variegata,* the infrequent *Sparganium fluctuans* and the uncommon *Nymphoides cordata. Myriophyllum tenellum* and *M. humile* may also be present in acidic waters, but their occurrence in the Berkshires is rare.

Acidic bedrock and shallow, rocky basins are important factors in the development of this community. In these waters, alkalinity measurements of up to 18 mg/liter HCO_3^- (Hellquist, 1980) indicate low alkalinity; the pH may be as low as 5.0. The waters are also low in nutrients. Lake and pond bottoms are typically rocky, gravelly or sandy and therefore not suitable for deep-rooted

plants. Margins are usually rocky, but may have peat or small areas of sphagnum bog along the edges. Conditions of clear and generally shallow water are conducive to growth of rosette-leaved plants. South Pond in Savoy State Forest has an excellent examples of this community.

Acidic Brownwater Lake/Pond Community

Like the preceding habitat, this community is found at the higher elevations in regions of acidic bedrock on the Berkshire Plateau. It is usually associated with bog habitats, or boggy areas that may have been altered or flooded.

The vegetation includes more species of the floating-leaved form, such as *Nuphar variegata, Nymphaea odorata, Brasenia shreberi, Sparganium fluctuans, S. angustifolium* and the rare *Nuphar pumila**. *Utricularia radiata* is quite common on the Plateau along with *U. vulgaris,* a widespread species present in a variety of habitats. *Utricularia purpurea* may occur in both the Clearwater and Brownwater habitats, while *U. geminiscapa* is more restricted to bog waters. *Potamogeton epihydrus* var. *ramosus* is fairly common in this habitat. *Eriocaulon pellucidum* and *Sagittaria graminea* occur in shallow waters at the margins.

Ecological factors here are similar to those of clearwater habitats, but depth of water, light penetration, and substrate differ. Alkalinity levels may range up to 30 mg/liter HCO_3^- (Hellquist, 1980). If the basin of the water body is deep, organic matter will accumulate and provide suitable substrate for deep-rooted aquatics. The water becomes discolored with accumulated dissolved organic acids and fine particles of organic matter, which reduce the amount of sunlight available for growth of plants of a submersed growth form (McVaugh, 1958). Lack of drainage also contributes to increased organic accumulation. Bog Pond in Savoy State Forest and the Spectacle Ponds in Sandisfield State Forest are good examples of this aquatic community.

Moderately Alkaline Lake/Pond Community

The aquatic community of this and the following type are found in regions with calcareous bedrock in the Central Valley Region and occur at elevational range of 221–391 m.

Potamogeton species that more often occur within an alkalinity

range of 18–73 mg/liter HCO_3^- include *Potamogeton spirillus, P. epihydrus* var. *ramosus* and *P. robbinsii,* which also inhabit less alkaline waters (Hellquist, 1980). *Potamogeton amplifolius, P. gramineus, P. natans, P. praelongus, P. obtusifolius, P. zosteriformis* and *P. epihydrus* var. *epihydrus* are found in progressively more alkaline waters. The pH of these waters ranges from 7.0 to 9.0. Other aquatics that occur in moderately alkaline waters are *Cerotophyllum demersum, Najas flexilis, Elodea canadensis,* and occasionally *E. nuttallii, Vallisneria americana* and *Ranunculus longirostris. Lemna trisulca* is found more often in alkaline situations, while *L. minor* and *Spirodela polyrhiza* are common and widespread in most water. *Nuphar variegatum* and *Nymphaea odorata* are commonly found here also, *Myriophyllum sibiricum* (= *M. exalbescens*) is occasional, and the adventive *M. spicatum* can become a troublesome weed.

The higher alkalinity of the water, which derives from streams and springs flowing through calcareous bedrock, is the most important factor in this community; edaphic factors are important also. Situated mainly in the valleys, where till, outwash or alluvial soil is abundant and more or less alkaline, ponds and lakes have accumulated thick layers of muck on the bottom. Examples of this habitat are Lake Garfield, which is less alkaline. Lakes Pontoosuc and Onota in Pittsfield, and Prospect Lake in Egremont have higher, yet moderate alkalinity levels.

Highly Alkaline Lake/Pond Community

This rich and diverse aquatic community is similar in most respects to the preceding one and shares most of the vegetational elements. The alkalinity levels range from 73 to more than 109 mg/liter HCO_3^- (Hellquist, 1980). The pH may range up to 10.7. This community is distinguished by several *Potamogeton* species that are more typically found in these waters. *Potamogeton pusillus* var. *pusillus, P. foliosus* and *P. illinoensis* are common, while *P. friesii** is very rare. The alien *Potamogeton crispus* inhabits nutrient-enriched, sometimes polluted waters. *Potamogeton nodosus* may be present, but is more often found in quiet sections of rivers and streams. *Potamogeton pectinatus* is restricted to the most alkaline waters, those with levels above 109 mg/liter HCO_3^- (Hellquist, 1980). The same is true of *P. hillii**, which has the greatest concentration of populations, world-wide, in Berkshire

County (Hellquist, 1984), and is frequent locally in cool waters of beaver ponds and small streams. *Heteranthera dubia* is common in many highly alkaline sites while *Megalodonta beckii,* which is fairly uncommon, also occurs in this habitat, at least in Berkshire County. Often plants in these waters are encrusted with marly deposits. Good examples of highly alkaline water bodies are Shaker Mill and Cranberry Ponds in West Stockbridge, Lake Buel in Monterey and Mill Pond in Egremont.

RIVERS, STREAMS AND SPRINGS

Rivers and streams may be characterized as high-, medium- or low-gradient, depending on steepness of slope; most have stretches of both fast and slow-moving waters. Rapid sections are often at the headwaters, which originate on the slopes of mountains and on the Berkshire Plateau. In the valleys, streams typically meander, and are bordered by wide floodplains. Vegetation of both the waters and immediate banks is discussed here.

High-gradient Stream Community

There is no distinctive vascular aquatic vegetation in these streams. Usually the riverbank vegetation reflects the surrounding forest type, but may tend to have more mesic species. *Carex torta* is commonly found among rocks along the shore. A few elements of a flood-scoured bedrock community, as described by Rawinski (1986), occur along the Deerfield River, such as *Sanguisorba canadensis, Aster johannensis, Andropogon gerardii, Rosa blanda* and *Trisetum triflorum* ssp. *molle.*

Medium-gradient Stream Community

These rocky or gravelly streams, which are typically quite shallow, also contain few distinctive vascular aquatic plants. *Callitriche heterophylla* often colonizes sites in the shallow, quieter waters of these streams, and a few floodplain tree species, such as *Platanus occidentalis* and *Salix nigra,* may occur on streambanks. *Lobelia cardinalis, Helenium autumnale* and *Rudbeckia laciniata* seem to be generally restricted to streambanks, while numerous gravel bars support a few weedy species.

Low-gradient Stream Community

The aquatic flora of deep, slow-moving waters, with alluvial banks and silty bottoms, is similar to that of the Moderately and Highly Alkaline Lake/Pond Communities, but fewer species are present. The Housatonic watershed has the highest alkalinity of any in New England (Hellquist, 1980). The Hoosic River and its tributaries, which are part of the Hudson River watershed, has the third highest alkalinity in New England. *Potamogeton epihydrus* var. *ramosus* and *P. amplifolius* inhabit less alkaline streams, while *P. nodosus, P. hillii** and *P. perfoliatus* occur in highly alkaline streams. The introduced *P. crispus* is common in more polluted streams. *Ceratophyllum demersum* and *Elodea canadensis* occur in shallow backwaters, while *Myriophyllum spicatum* tends to be found in deeper water. Shallow, muddy waters may be colonized by *Sparganium americanum* and *S. emersum,* both of which often exhibit long, ribbon-like floating leaves in faster moving currents, while becoming emergent and reproductive nearby on the stream margin.

The silt banks and bars associated with this stream type host a distinctive pioneer community limited to annuals, due to the instability of these bars. Commonly found species are *Lindernia dubia, Bidens cernua, Xanthium strumarium, Eragrostis pectinacea, E. hypnoides, Rorippa palustris* and *Cyperus aristatus*; less common are *Gratiola neglecta, Veronica anagallis-aquatica,* and the rare grass *Eragrostis frankii**.

Spring and Spring Run Community

This community is found throughout the county wherever water wells up as springs and forms small streams. Shaded springs have little vegetation. However, the adventive *Nasturtium officinale,* and native species such as *Veronica americana, Chrysosplenium americanum* and *Mentha arvensis,* are typically abundant in springs of sunny locations and along spring-fed streams.

WETLANDS

There is a great variety of wetlands in Berkshire County, ranging from forested swamps to open graminoid wet meadows and level bogs. Many elements of these communities have a considerable

latitude of occurrence. A community may contain elements of both acidic and calcareous associations; one community may grade into another as a series of vegetation zones. For example, a Forested Fen may surround a Lake Basin Graminoid Fen, with Shrub Fen elements extending into both communities. Or, very commonly, there may be a mosaic of communities occurring in small patches throughout a wetland area.

Important in influencing the occurrence of these communities is the degree of acidity or alkalinity of the water, which is influenced by its source, the underlying bedrock, and the soil type. Soil depth and amount of accumulated organic matter also significantly influences the type of vegetation. Drainage through the wetland, whether very little, as in bogs, or considerable, as in swamps, marshes and fens, is an important factor affecting the amount of organic accumulation and nutrient supply (Dansereau and Segadas-Vianna, 1952).

In the following discussion, swamps include both forested wetlands and shrub swamps; marshes are open wetlands dominated by emergent or graminoid species; bogs and fens are treated separately.

SWAMPS

Acidic Conifer Swamp Community

These swamps occur on the Berkshire Plateau (420–600 m elevation) on flats adjacent to bogs or streams. The dominant species are *Abies balsamea* and *Picea rubens,* or *Picea mariana*; *Tsuga canadensis* is also common. The ground is typically covered with a deep layer of *Sphagnum* spp. and other mosses; shrubs and herbaceous plants are sparse. Among the shrub species are *Nemopanthus mucronata* and *Ilex laevigata.* The small evergreen groundcover taxa include *Gaultheria hispidula, Linnaea borealis,* and *Coptis trifolia. Cornus canadensis, Carex disperma, C. echinata, C. folliculata* and *C. trisperma* are common on the mossy mat; *Smilacina trifolia* is occasional.

Although the soil surface is peaty, often there is little accumulation, and the mineral soil layer is typically thin and rocky, unless the forest has developed over the margin of an old bog. Pools of standing water occur between roots and in low places. Poor drainage, coupled with acidic bedrock, are factors that con-

tribute to the low nutrient condition of the soil. Wolf Swamp in New Marlboro is an example of a closed bog with a well-developed Acidic Conifer Swamp along the edge.

Acidic Hardwood Swamp Community

This community, often referred to as the Red Maple Swamp Community, is frequent in the county at lower elevations in poorly-drained acidic sites. It is dominated by *Acer rubrum,* which although abundant, does not typically develop into large trees as in mesic terrestrial sites. Other tree species include *Ulmus americana,* and usually *Pinus strobus* on the drier margins. *Quercus bicolor* and *Nyssa sylvatica* may occur in this community, but only in the extreme southern part of the county.

The forest canopy is somewhat open, and a variety of shrubs and herbaceous species are associated with this community. Typical shrubs include *Ilex verticillata, Viburnum lentago, V. cassinoides* and *Lyonia ligustrina,* and occasionally *Nemopanthus mucronata. Salix discolor* and *S. sericea* may occur in openings. Common herbaceous species include *Osmunda regalis, O. cinnamomea, Dryopteris cristata, Onoclea sensibilis* and *Carex stricta.*

Important factors influencing this community are acidic water, derived from acidic substrate, poor drainage, and nutrient-poor soils. Few tree species can tolerate both high water levels and low nutrient conditions. Tree species, such as *Acer rubrum* and *Pinus strobus,* which need sunny openings to regenerate, are well-adapted to this habitat and find little competition here. Although quite acidic, there is no accumulation of peat in this habitat.

Circumneutral Hardwood Swamp Community

Given the extensive calcareous deposits in Berkshire County, this community and other more calcareous ones are common throughout the county, except on the Berkshire Plateau. These swamps may occur along rivers or streams or at headwater sources of a stream.

The dominant trees are *Fraxinus nigra* and *Acer rubrum,* and occasionally *Quercus bicolor* in the extreme southern portion of the county. The understory tree *Carpinus caroliniana* is common while *Lindera benzoin* is usually the dominant shrub. Of the

herbaceous plants, the most typical are *Symplocarpus foetidus, Saxifraga pensylvanica, Veratrum viride, Solidago patula, Equisetum sylvaticum, Osmunda cinnamomea, Carex bromoides, Rubus pubescens* and *Platanthera psycodes.*

Important factors influencing the community are rate of flow and pH of the water. In this community, ground water approximating a neutral pH seeps to the surface and flows slowly toward a stream, constantly supplying nutrients to the plants and creating a seepage swamp (McVaugh, 1958). Levels of alkalinity higher than preceding wetland communities facilitate nutrient uptake and decomposition of organic material.

Acidic Shrub Swamp Community

This community is widespread in regions where waters and soils are acidic, thus is more extensive on the Berkshire Plateau; it occurs on margins of streams and in poorly-drained basins. The dominant species is usually *Alnus incana* ssp. *rugosa,* but a number of other shrubs occur, including *Ilex verticillata, Spiraea latifolia, Vaccinium corymbosum, Cephalanthus occidentalis, Myrica gale, Lyonia ligustrina, Viburnum cassinoides* and *V. recognitum.* A few tree species such as saplings of *Acer rubrum,* or, if on the Berkshire Plateau, *Abies balsamea* or *Picea rubens,* are usually present, as well as the small tree *Amelanchier arborea* and the vine *Clematis virginiana.* Herbaceous species include *Onoclea sensibilis, Osmunda cinnamomea, O. regalis, Glyceria striata, Carex gynandra* and *C. stricta.* Additionally, *Aster puniceus* and *Eupatorium maculatum* occur in openings.

This habitat is similar to that of the Acidic Hardwood Swamp; shrub swamps may be transitional to a forested type. Flooding or water level fluctuation may retard or reverse the tendency toward development of a swamp forest.

Circumneutral Shrub Swamp Community

This community typically occurs on the low margins of streams or ponds, where the alkalinity of the water is nearly neutral. It is widespread in the county, but is more common in the valley region. Dominant shrubs are *Cornus amomum, C. stolonifera, Salix discolor, S. sericea* and *S. eriocephala. Lindera benzoin* is important as a good indicator of less acid conditions, and tends

to be more abundant when slightly shaded, unlike the previously-named shrubs. *Rosa palustris* grows thickly along marsh edges, *Alnus incana* ssp. *rugosa* is present, but plants tend to be scattered, and the vines *Clematis virginiana* and *Solanum dulcamara* can be abundant. Among the herbaceous species, *Symplocarpus foetidus, Saxifraga pensylvanica* and *Solidago patula* are most distinctive of the community. Other common species are *Osmunda cinnamomea, Dryopteris cristata, Viola obliqua, Caltha palustris, Ranunculus hispidus* var. *caricetorum, Carex lacustris* and *Glyceria grandis.* Tree species, such as *Ulmus americana* and *Acer rubrum* may also occur.

As in other wetland communities, alkalinity of water and topography are the main factors affecting the composition of this community. The habitat is similar to that of Circumneutral Hardwood Swamp. This community may be successional, as described by McVaugh (1958), but extremely wet or flooded conditions, such as those caused by beavers, may preclude extensive tree growth, or even kill existing trees.

MARSHES

The vegetation of marshes is characterized by tall, emergent graminoid species and some broad-leaved species growing either in water or in saturated soil. There is adequate movement and drainage of water to supply nutrients and remove organic acids. The soil is a mixture of organic and mineral sediments (Dansereau and Segadas-Vianna, 1952).

Robust Emergent Marsh Community

This community is found in shallow water along streams, rivers, ponds and lakes throughout the county. It is dominated by tall emergents that are rooted in a thick layer of organic muck or deeper mineral soil. Waters and soil may vary from acidic to fairly alkaline, with the most common condition being intermediate, making it difficult to delineate two separate communities.

Typha latifolia is most common and typically present in most marshes. *Typha angustifolia* occurs in more alkaline sites or along roadsides experiencing significant salt runoff from winter road salting. Other common species more often seen in acidic marshes

are *Scirpus cyperinus, S. pungens, Sparganium americanum, Eleocharis smallii, Spiraea latifolia, S. tomentosa* and *Aster puniceus.* With increasing alkalinity, *Scirpus tabernaemontanii* (= *S. validus*), *S. acutus, Sagittaria latifolia, Pontederia cordata, Peltandra virginica, Alisma subcordatum, Equisetum fluviatile, Potentilla palustris, Sium suave, Cicuta bulbifera, Carex comosa, C. lacustris, Asclepias incarnata, Iris versicolor* and *Lysimachia terrestris* will be observed, along with the preceding species. *Acorus calamus* and *Sparganium eurycarpum* occur in the more alkaline habitats, as does *Sagittaria cuneata*,* which is found only in occasionally flooded oxbow ponds.

Depth and flow of water, and to a lesser extent the acidity or alkalinity of the water and substrate, as well as depth and texture of the substrate, are important factors influencing this community. Maximum depth of water for *Scirpus cyperinus* is approximately 50 cm (Kadlec, 1958), for *Typha latifolia,* approximately 60 cm (Grace and Wetzel, 1981). Higher alkalinity increases organic decomposition and nutrient availability. A slow water-flow allows accumulation of mineral and organic soil favoring growth of rhizomes and roots of these and other species associated with this community.

Acidic Graminoid Marsh Community

This community, associated with rivers, streams and ponds, becomes established in very moist to saturated soil that is usually above water level in the latter part of the growing season. It occurs more often in the poorly-drained areas of the Berkshire Plateau, where broad, shallow margins of acidic ponds and streams provide much of this habitat type.

The vegetation is dominated by a variety of grasses and sedges, the most typical being *Calamagrostis canadensis, Glyceria canadensis, Carex stricta, C. folliculata, C. lurida, Dulichium arundinaceum, Scirpus cyperinus* and *S. atrocinctus.* Other common species are *Triadenum virginicum, Juncus canadensis, J. brevicaudatus* and *Eupatorium perfoliatum.* Smaller species that may exist in openings are *Eleocharis obtusa, Hypericum boreale, Lycopus uniflorus* and *Gratiola neglecta.*

Flat stream valleys with acidic bedrock, acidic waters and infertile soils contribute to the formation of this vegetation type.

Many of these marshes develop from silted-in, abandoned beaver ponds.

Circumneutral Graminoid Marsh Community

This community, more often found along streams and rivers in the valley region where substrate and water tend to be more alkaline, is more diverse than that of the previous community, with a greater variety of sedges and forbs.

The common grasses include *Calamagrostis canadensis, Phalaris arundinacea, Glyceria grandis, G. borealis* and *Leersia oryzoides.* Common sedges are *Carex lacustris, C. stipata, C. vulpinoidea* and *C. comosa,* as well as the rarer *C. trichodcarpa**, common only in Hoosic River swales. *Eleocharis intermedia** may occur on open mud margins. *Iris versicolor* and *Angelica atropurpurea* are common in this, and many other, wetland types. *Acorus calamus* and *Juncus nodosus* occur in nutrient-rich sites. Many smaller forbs occur between the graminoids or at marsh edges, such as *Thelypteris palustris, Boehmeria cylindrica, Scutellaria galericulata, Campanula aparinoides, Penthorum sedoides, Verbena hastata, Mimulus ringens, Lysimachia thyrsiflora, Asclepias incarnata* and *Solidago uliginosa.*

Water and soil of circumneutral alkalinity, topography and development of thick swamp muck, are important factors influencing the distribution of the community.

BOGS

Level Bog Community

The acidic bog is a well-defined, often-studied community distinguished by a floating *Sphagnum* mat and dominated by ericaceous shrubs. This ombrotrophic peatland is most often found on the Berkshire Plateau in poorly-drained basins associated with acidic bedrock at elevations averaging 520 m. At least one bog occurs in a sandy outwash underlain by clay at an elevation of 213 m in Sheffield (Oltsch, 1974).

The vegetation may occur in a regular series of zones from an open water pond in the center to a forested zone at the edge of the bog (Crow, 1969). When lacking an extensive *Sphagnum* mat, elements of these zones may be clustered in an irregular pattern

around the outer edge. The species composition of these zones varies from one bog to another, but certain species are almost always present. *Chamaedaphne calyculata* and *Decodon verticillata* are common at the inner edge along the pond edge, their intertwined stems and roots forming a base for the beginning of a *Sphagnum* mat. If there is a broad *Sphagnum* mat, sedges such as *Carex limosa, C. paupercula, C. canescens* and *C. lasiocarpa* occur along with *Eriophorum virginicum, E. tenellum, E. vaginatum, Cladium mariscoides* and *Scheuchzeria palustris**. Other species common on the mat are *Vaccinium macrocarpon, V. oxycoccos, Sarracenia purpurea, Rhynchospora alba* and *Drosera rotundifolia. Pogonia ophioglossoides* is fairly common, while *Calopogon tuberosus* and *Platanthera blephariglottis* are less so. In open, peaty, shallow pools, *Xyris montana, Drosera intermedia, Utricularia cornuta,* and occasionally *U. gibba* occur. *Picea mariana* and *Larix laricina* occur as scattered, stunted trees, and in small clumps on the mat, but become denser and taller at the outer bog edge. The bog heaths, *Andromeda glaucophylla, Kalmia polifolia* and *Ledum groenlandicum* may form a large shrub zone nearer to the outer edge along with *Myrica gale. Calla palustris* commonly grows in *Sphagnum* among the heaths, while *Smilacina trifolia* occurs occasionally. There may be an abrupt change to upland woods, or bog shrubs may give way gradually to swampy coniferous woods; a moat may also occur at the outer edge.

Several factors affect formation of the typical level bog, including acidity, nutrients, water flow, basin depth, and climate. Ombrotrophic bogs have little inflow or outflow, and are dependent on rainfall for the few nutrients that enter the system (Heinselman, 1963). Berkshire bogs range from those with absolutely no inflow to those fed by small streams from a limited watershed. Lack of drainage leads to accumulated organic acids that retard decomposition of organic material (Dansereau and Segadas-Vianna, 1952). *Sphagnum* moss actively produces acidic conditions (Andrus, 1980), and strongly influences the vegetation patterns.

Characteristic of cold basins, temperature measurements taken in a Massachusetts bog (542 m elevation) by Moizuk and Livingston (1966) showed that the bog mat experienced approximately one-third the number of frost-free days as was recorded in the surrounding forest. They also determined that nutrient deficiencies hindered *Acer rubrum* from invading the mat. Those conditions, and the instability of the bog mat, may retard or

prevent succession to a closed bog forest. Larsen (1982) indicates that succession may take an irregular course, which can be reversed, or can diverge toward a variety of associations.

FENS

Fens differ from bogs in several ways. Cold water, seeping up through calcareous bedrock, becomes highly alkaline and moves slowly through the community toward a small stream (Schwintzer, 1978, 1981). High levels of minerals are constantly supplied. A floating mat may develop, but it will be dominated by sedges and grasses. *Sphagnum* is typically absent, but may appear as small patches and hummocks, accompanied by other bog vegetation. There are a variety of fen community types, ranging from those that are peatland communities to those lacking peat, and they may exist as a mosaic or in definite vegetation zones. The species composition of fens is rich and diverse, containing many plants rare for the state. A preponderance of fen communities in Massachusetts is found in southern Berkshire County, because of its extensive calcareous bedrock and more level terrain.

Forested Fen Community

Influenced by highly calcareous water, this peatland community is found more frequently in the southern half of the county, and is usually associated with other fen communities. These fens tend to occupy edges of level basins or margins of extensive, flat areas along gently flowing streams in open valley bottoms.

Species composition of the tree layers shows considerable variation from site to site, there being both hardwood and conifer elements that are important. *Larix laricina* is the dominant conifer, and in the valley region it seems to be an indicator of fen conditions. *Fraxinus nigra* is always present, and *Acer rubrum* commonly occurs as well. *Quercus macrocarpa** is common in the southern part of the county. In some fens *Tsuga canadensis* is one of the dominant trees. *Thuja occidentalis**, while never common, is very rare at present, possibly because it was thoroughly harvested in earlier times.

In forested fens, trees are typically scattered, thus the canopy is usually open. Fen shrubs such as *Salix candida* and *S. serissima*, *Rhamnus alnifolia* and *Potentilla fruticosa* occur in open areas.

These species are good indicators of highly calcareous situations. *Ribes triste** occurs in shaded wet areas. Shrubs typical of acidic bogs such as *Andromeda glaucophylla* and *Ledum groenlandicum* occur only on *Sphagnum* hummocks raised above, and isolated from, the calcareous water. In muddy, bare openings, small herbaceous species such as *Lobelia kalmii,* and rarities such as *Malaxis brachypoda** and *Rhynchospora capillacea** occur. Other species associated with Forested Fens are *Cypripedium calceolus* var. *parviflorum**, *C. reginae**, *Pyrola asarifolia**, *Conioselinum chinense** and very rarely *Petasites frigidus* var. *palmatus**.

The presence of a number of northern species found in fens may be due to the cold groundwater, which has provided a stable, cool habitat. Fens along Schenob Brook in Sheffield are among the most extensive and significant.

Shrub Fen Community

This community is found in association with other peatland fen communities, either intermixed or as a zone at the edge. The dominant and characteristic shrubs are *Salix candida, S. serissima** and *Potentilla fruticosa,* an important indicator plant of any calcareous situation, wet or dry. The small shrub *Rhamnus alnifolia* is also a reliable indicator of fen conditions; other common shrubs are *Toxicodendron vernix* and *Ribes hirtellum. Lonicera villosa* occurs most often in association with fens. The small tree *Betula pumila** occurs at the edge of shrub fens and in open graminoid fens, along with small specimens of *Larix laricina.* The shrub layer has many openings where herbaceous species such as *Geum rivale, Lysimachia thyrsiflora, Galium labradoricum**, *Solidago patula, Cirsium muticum, Symplocarpus foetidus* and *Carex interior* occur. *Carex castanea**, a rare northern species, occurs at edges of shrub fens.

Sloping Graminoid Fen Community

This peatland community, often referred to as a calcareous wet meadow, occurs in calcareous areas throughout the central valley region of the county, but more often in the southern two-thirds, and is found on the sloping edge of other fen communities. Many of its species, restricted to this community, are rare in the state.

Sedges dominate this community, with the common species being *Carex flava, C. granularis, C. lanuginosa* and *C. aurea.* Rare species include *Carex alopecoidea**, *C. chordorrhiza**, *C. sterilis** and *C. tetanica**. *Scirpus pendulus** may be locally abundant in these rich meadows. The most common cotton-grass is *Eriophorum viridicarinatum*; less common is *E. gracile**. *Muhlenbergia glomerata* is typical of these fens. The rare *Cardamine pratensis* var. *palustris** occurs in small pools between sedge tussocks. Other indicative herbaceous species are *Geum rivale, Galium boreale**, *Lobelia kalmii, Parnassia glauca, Gentianopsis crinita* and *Solidago purshii.* Both *Liparis loeselii* and *Sisyrinchium mucronatum** are restricted to, yet uncommon in, this community. Usually, small individuals of the shrub fen are also present here, such as *Rhamnus alnifolia, Salix candida* and *S. serissima* and saplings of *Larix laricina,* indicating that without some form of disturbance, shrub fen elements would become more common. Many of these sloping fens are presently maintained as pastureland or by mowing at various times.

Lake Basin Graminoid Fen Community

This rare community occurs on extensive, flat, former lake basins that have become filled with peat, and is influenced by highly alkaline water from both ground water and adjacent small streams. Elements of the sloping graminoid fen, the shrub fen and forested fen communities surround the open, flat sedge-dominated mat. Bog elements are also present. The open flats adjacent to pond and stream are dominated by *Carex aquatilis* and *C. lasiocarpa,* typical of minerotrophic fens (Schwintzer, 1978; Larsen, 1982). *Scirpus acutus* and *Cladium mariscoides* occur at the pond edge. *Typha latifolia* occurs scattered throughout the sedge flats. Small, open, muddy sites contain *Eriophorum alpinum* (= *Scirpus hudsonianus*) and a rare, northern species, *Eleocharis pauciflora**. *Utricularia intermedia* occurs in shallow channels. The shrub *Myrica gale* is also present. Shrubs typical of fens, such as *Salix pedicellaris, S. candida* and *Potentilla fruticosa* occur scattered, while *Betula pumila** is part of the shrub fen that borders the sedge flat. Bog species, such as *Calopogon tuberosus, Pogonia ophioglossoides, Sarracenia purpurea, Andromeda glaucophylla, Carex limosa* and *Vaccinium macrocarpon* occur in scattered patches of *Sphagnum.* The one excellent example of this com-

munity in the county is Kampoosa Fen in Stockbridge, from which this description is drawn.

The broad basin topography allows the accumulation of a large expanse of peat, enabling the community to form an extensive and fairly uniform association. The resulting flat topography may not be as well drained as in other fen systems, and areas that are more remote from water flow may develop accumulations of *Sphagnum* and other acidophilic bog species (Larsen, 1982; Schwintzer, 1981).

Calcareous Seep Community

This is a small, unusual and distinctive community found throughout the county where cold, calcareous water seeps to the surface and forms small rivulets that, at times, flow just under the soil surface. It usually occurs on slopes in rocky or gravelly soil; no peat accumulates.

The vegetation consists mainly of sedges and other low graminoids and herbaceous species. *Parnassia glauca* is an indicator plant. *Equisetum hyemale* or *E. variegatum* often forms dense, pure stands; *E. scirpoides** occurs on cool, moist, mossy surfaces. Various species characteristic of other fen communities are also present here, such as *Carex aurea, C. granularis, C. leptalea, Muhlenbergia glomerata, Malaxis brachypoda**, *Cypripedium reginae**, *Spiranthes cernua, S. romanzoffiana**, *Lobelia kalmii* and *Petasites frigidus* var. *palmatus**.

The slope and flowing ground water create an unstable situation where trees seldom persist beyond the sapling stage, therefore perpetuating the sunny openings that can be colonized by small fen species requiring at least some sun. *Cypripedium reginae**, for example, may be shaded out in forested fen habitats, while in this community, it may persist indefinitely.

SUMMARY

The floristic diversity of the county is illustrated by the recognition of 35 major plant communities. Of primary importance influencing the development of these diverse communities are the underlying bedrock and the topographical heterogeneity of the county, climate, local microclimatic conditions, groundwater pH and alkalinity, and soil nutrient levels. Important also is the di-

versity of the pool of species available to colonize these habitats, and the post-glacial history of plant migrations into New England.

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DEPARTMENT OF PLANT BIOLOGY
UNIVERSITY OF NEW HAMPSHIRE
DURHAM, NH 03824

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NEW ENGLAND NOTE

PERSISTENCE OF *CAREX CARYOPHYLLEA* (CYPERACEAE) IN MASSACHUSETTS

L. A. STANDLEY

The European sedge, *Carex caryophyllea* Latourr. (section *Mitratae* Kukenth.), has been introduced into several areas of the northeast. Herbarium records indicate that this species became widely established in Massachusetts (Essex County, Norfolk County, Suffolk County, and Worcester County), with single records from Maine (Portland), Washington, DC, New York (Dutchess County), and New Brunswick (Albert County). The majority of herbarium records date from 1860 to 1905, but the earliest collections appear to be from the early 1800's in Massachusetts. With one exception (Palmer, 1935) I have seen no records for collections made after 1905 from Massachusetts sites.

In conjunction with treatment of the section for *The Flora of North America,* I attempted to determine whether this introduced species was persistent in Massachusetts by searching all localities for which there was sufficient label information. Ten sites were examined in Essex County, Suffolk County, and Norfolk County; of these, populations appear to have been extirpated in Salem, Westwood, Needham, and West Roxbury, but were re-located at Dedham, Norwood, and Boston localities. No new localities were found during 1991.

Two small patches of *Carex caryophyllea* were located near the Downey School, Downey St., Dedham (*Standley 1749*), a site for which the previous record was in 1897 (*S. K. Harris s.n.*). A large population was located near the Xaverian High School on Clapboardtree St. in Norwood (*Standley 1750*), for which the previous record was 1884 (*T. O. Fuller s.n.*). A small population was located in the Arnold Arboretum, Jamaica Plain, on Peters Hill in the *Sorbus* collection (*Standley 1761*), for which the previous record was 1932 (*E. J. Palmer 40185*). Vouchers are deposited at NEBC.

Carex caryophyllea is widely distributed in Europe in dry, grassy or rocky soils (Chater, 1980), although it is generally restricted to chalk or limestone grassland in Britain (Jermy et al., 1982). Where it persists in Massachusetts, it occurs in habitats similar to *C. pensylvanica* Lam., including dry roadsides, margins of woods,

old dry pastures, and areas of poor soil in fields from which taller grasses (*Dactylis glomerata* L., *Poa pratensis* L.) appear to be excluded. Where it has been extirpated, development or other disturbance appears responsible; where not eliminated by disturbance, *C. caryophyllea* has been able to persist successfully for over 100 years, but has not colonized new sites. This finding suggests that reproduction is primarily vegetative, and that despite abundant flowering and seed set, this introduced species has not become weedy.

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THE NEW ENGLAND BOTANICAL CLUB
22 Divinity Avenue
Cambridge, MA 02138

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Rhexia virginica L., meadow beauty, is found from Nova Scotia to Georgia, but is rare at the northern limits of its range. The only northern outlier of the tropical family Melastomataceae, it has distinctive 3-veined leaves and geniculate stamens. Original artwork by Josephine Ewing.

Rhodora

JOURNAL OF THE
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Vol. 94 July 1992 No. 879

SYMPOSIUM PROCEEDINGS

NEW ENGLAND PLANT CONSERVATION: THE SCIENTIFIC BASIS FOR EFFECTIVE ACTION

March 21, 1992

Bentley College, Waltham, MA

presented by

THE NEW ENGLAND WILD FLOWER SOCIETY
and
THE NEW ENGLAND BOTANICAL CLUB

with additional support from

THE SURDNA FOUNDATION

Symposium Committee

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RHODORA, Vol. 94, No. 879, pp. 215–217, 1992

NEW ENGLAND PLANT CONSERVATION: THE SCIENTIFIC BASIS FOR EFFECTIVE ACTION

FOREWORD

LESLIE J. MEHRHOFF, President
New England Botanical Club
and
WILLIAM E. BRUMBACK, Conservation Director
New England Wild Flower Society

On March 21, 1992, the New England Botanical Club and the the New England Wild Flower Society co-sponsored a symposium entitled New England Plant Conservation: The Scientific Basis for Effective Action. This symposium was held at Bentley College in Waltham, Massachusetts, and was attended by 175 botanists, conservationists, and others concerned with the welfare of our native flora from all over the northeast. The four papers from the symposium are presented in this issue of *Rhodora*.

As with any successful symposium, much work went into its preparation. Almost two years ago, the New England Botanical Club asked Lisa Standley to chair a committee to plan this symposium, jointly sponsored by the Club and the New England Wild Flower Society. In addition, the committee consisted of William Brumback, W. Donald Hudson and Leslie Mehrhoff. The committee was given a valuable boost when the New England Wild Flower Society hired Frances Clark as Conservation Program Officer. Frances kept us all on track, aided in the correspondence and served as tireless agent for the committee.

The symposium initiative was given further impetus by the recently formed New England Plant Conservation Program (NEPCoP), a voluntary collaboration of representatives from over sixty organizations, agencies and universities already working to protect endangered flora throughout the region. NEPCoP examines both *in situ* and *ex situ* conservation strategies and encourages cooperative action to prevent regional extirpation and to promote recovery of endangered species in the wild. The symposium committee's intention was to bring the most up-to-date information to four areas of the decision-making process where

science is most needed. This focus is the rationale for the sequence of papers. We begin with those all-too-familiar taxonomic questions that plague most conservationists, proceed to the difficulties of deciding which taxa to protect, address the processes involved in effective habitat management, and finally finish with the "sticky wicket" of *ex situ* conservation and reintroductions.

Unlike many symposia with lots of speakers and little time for interaction between the speakers and those in attendance, from the onset this symposium revolved around the idea that much would be gained from offering ample time for audience participation. Each of the speakers would be part of a panel, with a moderator and two or three panelists to respond; after the responses, the moderator was to take questions for any panelist from the floor. This format facilitated discussion and set the groundwork for further discussions during the breaks which followed each presentation.

While time and expediency prohibited us from including panelist's response and comments from the audience with each presentation, speakers had the option of incorporating these responses or comments into his or her paper. We would like to thank the following formal participants for their input to the symposium:

Taxonomic Issues and Rare Plant Protection:
Gregory J. Anderson (moderator), David Barrington and Susan von Ottingen
Setting Priorities for Regional Plant Protection Programs:
Jeanne Anderson (moderator), Anne Hecht, Leslie J. Mehrhoff and Robert E. Zaremba
Habitat Management:
W. Donald Hudson (moderator), Peter W. Dunwiddie, Susan C. Gawler and Harry R. Tyler
Reintroduction Dilemma:
Barbara St. John Vickery (moderator), William E. Brumback and Mary J. Parkin

The New England Plant Conservation symposium was supported by the New England Botanical Club, the New England Wild Flower Society, and a grant from the Surdna Foundation. Publication costs were supported by the New England Botanical Club with generous contributions from the speakers and panel participants.

L.J.M.
CONNECTICUT GEOLOGICAL AND
NATURAL HISTORY SURVEY
BOX U-42
THE UNIVERSITY OF CONNECTICUT
STORRS, CT 06268

W.E.B.
GARDEN IN THE WOODS
180 HEMENWAY ROAD
FRAMINGHAM, MA 01701

RHODORA, Vol. 94, No. 879, pp. 218–242, 1992

Symposium Paper No. 1

TAXONOMIC ISSUES IN RARE SPECIES PROTECTION

LISA A. STANDLEY

ABSTRACT

Taxonomy provides the basis for rare species protection by defining and naming the taxa eligible for listing and by providing biological information critical to plant protection. As endangered species laws become stronger (or more restrictive, depending on the point of view), it will become increasingly important that lists of endangered species be based on a solid scientific foundation and incorporate correct nomenclature. These factors are also important on a regional basis and facilitate coordinated interstate plant protection efforts. However, an examination of endangered species lists in the New England states has shown that 30% of the listed names demonstrate taxonomic inconsistency or error, and that additional biological problems of hybridity or asexual reproduction occur that may not be consistent with state endangered species definitions. The majority of the taxonomic problems noted in the New England rare flora are at the infraspecific level. Specific policy recommendations which arise from this study include the addition of synonyms to state endangered species lists, the formation of scientific advisory boards to assist state agencies with evaluating taxonomic changes, and increased support of taxonomic research dealing with rare species issues.

Key Words: Rare plant species, New England

INTRODUCTION

Taxonomy is fundamental to rare species protection, as this science determines the circumscription and name for a taxon. Taxa must be identified, delineated, and named before determination can be made whether they are rare and/or endangered. In order to implement necessary protective measures, starting with an official listing of rare and endangered species, these taxa must have valid and usable names. "Valid," as used here, means that names must conform to the International Rules of Nomenclature and reflect the best available biosystematic studies. "Usable" means that names, as stated on rare species lists, must also enable amateur and professional botanists to correctly characterize a plant's rare and endangered status.

Although taxonomy is the basis of rare species protection, taxonomic change is the source of some of the largest problems in conservation. Our knowledge and understanding of the evolutionary relationships of plants is incomplete, even in New En-

gland. As noted by Kartesz and Kartesz (1980), considerable taxonomic work is needed:

> "To untangle completely the collective nomenclatural web of truth, error, and synonymy which has accrued to the flora of North America will require years of detailed taxonomic research by individual specialists. Even in the Northeast, where vascular plant systematics has been an active interest for well over two centuries and where the amount of botanical exploration is unparalleled anywhere in the Western Hemisphere, many nomenclatural and taxonomic uncertainties still prevail."

Taxonomic revision benefits rare species management and protection efforts since it provides information on the biology of the rare species and their evolutionary relationships, and clarifies the taxonomic status. However, taxonomic revision creates problems for rare species protection when the name and/or status of each individual taxon undergoes change and revision. Lists of protected organisms need to keep pace with, and evaluate, taxonomic and nomenclatural changes.

These changes may create legal problems. If a listed rare taxon is protected under a certain name, that name must be correct and in conformance with other published names. Users of a rare species list must be able to identify plants and match their identification with a name on the protected list. A list cannot simply use the most recent name for a taxon, since this procedure would allow unscrupulous collectors to use an older name. As rare species are increasingly protected by legal statutes which affect private property, challenges to species listing are inevitable. Use of the appropriate taxonomic methods reinforces and supports efforts to provide protection to threatened flora.

In this paper, I examine the kinds of taxonomic and biological problems which exist in rare species lists published for the New England states, target research needed to solve some of these problems, and suggest other ways that scientists and regulators can interact to promote the preservation of rare taxa.

TAXONOMIC CONCEPTS

An interest in the diversity of plants is the primary reason why most botanists have taken up the study or protection of plants,

as either a vocation or avocation. For most of us, the rare taxa of plants are especially intriguing for several reasons. Once one becomes familiar with the common species, searching out these real treasures of the plant kingdom becomes a challenge with intrinsic rewards. From a scientific point of view, rare taxa are of particular interest. Scientists approach the world by asking questions, and rare organisms provide the opportunity to ask a lot of questions: why is this thing rare? How, and from what, did it originate? What other species is it most closely related to? What aspects of its biology are unique?

The science of taxonomy is more often called Biosystematics, and its objective is the understanding of the pattern and process of evolution. Biological diversity itself, the numbers and kinds of organisms, is the pattern which results from this evolutionary process, understanding this pattern is critical to understanding the evolutionary process. Biosystematics involves three closely integrated aspects of scientific study.

Taxonomy is the science which attempts to determine the pattern resulting from evolution. A taxonomic study is based on compiling data from morphology, anatomy, cytology, genetics, reproductive biology and distribution, and analyzing these data to determine patterns of similarity and variation within and among populations. Data come from herbarium collections as well as living populations. The analysis may be based on an intuitive or computer-assisted analysis, but in either case it attempts to identify similar populations and to determine the similarities or disjunctions among population groups. The end result is a classification based on similarity and difference.

Nomenclature is the process by which each taxon identified and circumscribed by the taxonomic process is assigned a unique and correct name according to the current rules of nomenclature. This process is really not scientific, in the sense that no hypotheses are generated or tested, and relies on library and herbarium resources.

Biosystematics is the science which attempts to determine the evolutionary relationships among the taxa which are circumscribed in the taxonomic phase of the study. The data used may be the same as those used in taxonomy, but are here viewed from a different perspective: that of the analysis of characteristics as shared or not, as ancestral or derived. Data are evaluated, again either by intuitive analysis or assisted by computer programs.

This process refines the analysis of evolutionary pattern, connecting the taxonomic units in ancestor/descendant relationships. This stage enables good questions about evolutionary processes to be asked, since the results are evolutionary units and their relationships. Based on this level of information, scientists can proceed to study how the process of evolutionary divergence may have occurred.

The results of biosystematic/taxonomic studies are reported in scientific papers, monographs, theses, floras, and checklists. Such studies are fundamental to rare species protection, since they identify the taxa to be protected, assign names to be used in listing and identification, and provide biological data for protection and management.

How good are the taxonomic data available to us? Is a classification, whether published in a master's thesis or the most up-to-date regional flora, The Truth? We need always to keep in mind that the results of any taxonomic study are hypotheses, and the accuracy of one or another hypothesis depends on the kinds of evidence used, the types of analysis applied, and the competence of the researcher. Any taxonomy is subject to scrutiny, because it is a collection of scientific hypotheses. Classifications are constantly undergoing revision, as successive "generations" of botanists use older classifications as hypotheses to be tested using new evidence, new methods, new ways of thinking about plant evolution and classification. A classification scheme is not, and will never be, a stable or static entity, nor can we expect it to be such.

You should note that I have been using the word "taxon" rather than species. Taxon means, in a vernacular sense, a "kind" of a plant—"taxon" is any distinct biological unit, regardless of rank. Formal taxonomic ranks include family, genus, species, subspecies, and variety in addition to other less-used ranks such as subfamily, tribe, subgenus and section. Each rank has a generally-accepted meaning regarding the degree of similarity among members of that rank, and the amount of difference between different taxa at the same rank, although this variation depends to some extent on the plant family in question. For example, sections in the genus *Carex* are about as distinct as most genera in the Poaceae. We think of rare species lists as including and protecting most kinds of plant taxa; however, this assumption is not explicitly true for all rare species lists.

Most New England state laws are in fact inclusive of taxa at all ranks below the level of genus. In the Connecticut statute, " 'Species' means any species, subspecies, or variety of plant or animal, and includes any distinct population segment of any animal or plant." Massachusetts is similarly inclusive: " 'Species' means any distinct plant or animal population whose members interbreed or cross pollinate when mature and can include any subspecies or variety of plant or animal." New Hampshire also defines species to include "any species, subspecies, or variety of plant."

Rhode Island and Vermont also apparently include all ranks, although these are not named specifically. In the Rhode Island statute, " 'Endangered species' shall mean . . . any animal or plant." In Vermont, rare " 'Species' includes all subspecies of wildlife or wild plants and any other group of wildlife or wild plants of the same species, the members of which may interbreed when mature."

However, some laws include only some taxonomic ranks and generally exclude the plant rank "variety." The Maine statute does not provide a formal definition of species; however, all definitions refer to "a plant species or subspecies." The Federal statute defines endangered species as "Any species, including any subspecies of fish or wildlife or plant, and may include distinct population segment of any species of vertebrate, fish, or wildlife which interbreeds when mature." Ayensu (1984) has pointed out that the Federal list does currently include taxa at the varietal rank and notes that such listings may be subject to legal question. The U.S. Fish and Wildlife Service considers, since subspecies and varieties are essentially synonymous in meaning, that taxa named at the varietal rank are validly listed. None of these statutes explicitly provide endangered species status to hybrids, although the Rhode Island statute may be interpreted as including hybrids.

As a taxonomist, I see an additional problem with several of these definitions, particularly with the Connecticut, Vermont, Massachusetts, and Federal definitions, which allow protection of "any distinct population segment" (Vermont) or "any distinct population" (Massachusetts). These laws allow the protection of populations or segments of populations within species which have never received a formal taxonomic name. How does one identify and protect something which has no name? A more serious question concerns the evidence that the population or segment is sufficiently distinct to warrant protection. North-temperate plants

have been fairly extensively studied during the last century. Our experience in New England has been that if there is even the slightest indication that a population is morphologically distinct, someone will have assigned it a name. Gray's Manual (Fernald, 1950) is full of such segregate taxa. If no name at any recognized taxonomic rank is available for a population or segment, can and should it be protected?

The concepts which lie behind the assignment of taxonomic ranks are important to rare species conservation. Managers and regulators need to know the basis of the classification with which they are dealing. In addition, several of the legal definitions of endangered species incorporate species concepts. Since so many of the endangered species statutes include taxonomic ranks, and in some cases explicitly define the biological characteristics of that rank, it is useful at this point to summarize some of the taxonomic concepts that underly the definitions of ranks.

Species Concepts

A taxonomist's work is based on a specific concept of what a species is; this concept provides a working theoretical framework. Numerous species concepts have been developed historically and have been the source of much debate. However, there is no ultimately correct definition of "species." Rather, different concepts are useful for different approaches to taxonomic or evolutionary studies (Liden and Oxelman, 1989).

The biological species concept (BSC), now often referred to as the isolation concept, is most familiar to non-scientists although often in an inaccurate form. At some stage of their education, most people have learned that, according to the biological species concept, two species cannot interbreed and produce fertile offspring, as shown by the horse/donkey/mule example. Mayr (1963) formulated the BSC to state that species are "groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups." This rather rigid and limited definition is probably the exception rather than the rule. While most species do not interbreed in nature due to some sort of isolating mechanism, speciation and reproductive isolation are evolutionarily independent (Endler, 1989). Adherence to this definition does allow recognition of cryptic species which differ by few phenetic characters but which are reproductively isolated due

to genetic/behavioral traits. Populations of the same species may be more effectively isolated by distance than populations of different species may be isolated by other mechanisms. Natural hybridization in plants may be frequent, as evidenced in the fern genus *Dryopteris,* where *D. celsa, D. goldiana,* and *D. clintoniana* all are known to cross (Barrington et al., 1989).

The biological species concept carries another aspect, that of reproductive cohesion. Some authors segregate this aspect as the "cohesion" concept, but it is explicit in Mayr's more recent definition (1982) which states that a species is "a reproductive community of populations that occupies a distinct niche in nature." Members of a species reproduce themselves, and phenotypic cohesion among populations of a species may be maintained by genetics, reproductive constraints, or selection. This cohesiveness also carries an ecological component, indicating that species are ecologically distinct.

The application of a species concept which emphasizes cohesion, rather than isolation, is generally applicable to plants. It is also inclusive of plants which do not reproduce through normal sexual means by deleting the requirement that species are groups of actually or potentially interbreeding populations.

Although the biological species concept is, in some form, the theoretical basis for systematics, it is rarely used in practice as it requires extensive breeding studies and genetic studies of populations. Except in some long-term biosystematic studies, these data are generally not available. Reproductive continuity, and isolation, are inferred based on other characteristics and discontinuities between taxa. States which incorporate a biological species concept into protection statutes should be concerned about defending the listing of individual taxa based on reproductive biology.

Several endangered species laws (Federal, Massachusetts and Vermont) define an endangered species as "any population . . . whose members interbreed or cross-pollinate when mature." This definition is a strict and rather limited application of the cohesion concept of plant species, which I have not been able to locate anywhere in the literature dealing with species concepts; it effectively excludes all apomictic or asexual species or populations, as well as all species or populations which are exclusively autogamous (selfing). *Phegopteris connectilis,* listed in Rhode Island, is reported to be an apogamous tetraploid and should therefore be

excluded from the list. *Antennaria petaloidea,* listed in Connecticut, is also apomictic and could not be listed in Massachusetts. Similarly, *Arnica lanceolata,* listed in New York, Maine, and New Hampshire, is an apomictic tetraploid which would be excluded from listing elsewhere in New England based on its lack of outbreeding. Many members of the rosaceous subfamily Maloideae, including *Amelanchier* and *Crataegus,* are at least facultative apomicts (Campbell and Dickinson, 1990). *Cratageus bicknellii,* although listed in Massachusetts, may not be legally eligible as a species based on research on other members of *Crataegus* section *Rotundifoliae* which has shown that these taxa are facultative apomicts (Smith and Phipps, 1988).

Most often in taxonomic practice, species are recognized using phenetic concepts. Species are recognized in part by the similarity among individuals and populations, observed as the low levels of variation present within and among populations. In simple terms, members of a species resemble each other more than they do members of any other group. The second key criterion is discontinuity between species. A species is everywhere distinct from other species, without extensive intermediate forms or hybrids. In general, this distinction is the practical method of taxonomy, supportable because it is based on kinds of evidence normally used in taxonomic studies. It is the logical result of the kinds of methods of analysis used in taxonomic studies, whether groups are created by piling herbarium specimens or by complex computer-aided multivariate analysis. When used in a thorough biosystematic study, the determination of taxa using phenetic methods is a valuable step in that it constructs a hypothesis which can be tested for the applicability of the isolation and cohesion concepts of species. Most, perhaps all, existing floras and checklists are based on phenetic species concepts and a phenetic-based taxonomy. Those endangered species laws which are based on phenetics, or which simply protect taxonomic categories without invoking species concepts, are legally defendable.

Infraspecific Taxa: Subspecies vs. Varieties

Generally, most taxonomists recognize taxa below the level of species, but historically, there have been some exceptions. Mackenzie (1931–35), in his treatment of *Carex* for the North American flora, only recognized taxa at the level of species. Two in-

fraspecific taxonomic ranks are generally used, the subspecies and the variety. Variety is the older usage and originally referred to any minor variant of a species. This rank was used for populations or individuals which differed from the species in one or a few characters or which occurred in a distinct area or habitat.

Subspecies had its origin in zoological taxonomy and was used for "incipient species," geographic races generally distinct from other populations in a few characters but which intergraded in zones of contact. In these subspecies, viewed as incomplete stages in evolution, divergence was not complete and innate reproductive isolation had not been attained. The term "subspecies" has only recently, and not universally, been adopted for plants, although it is the only infraspecific rank used in zoological nomenclature.

The term "variety" has had mixed usage in plants. Originally, "variety" meant any marked variation within the species, not necessarily geographic, and was generally the only rank used for infraspecific taxa, whether variation had a geographic, ecological, or merely morphological basis. "Variety" was often used simply to indicate minor, not necessarily consistent, morphological variation. Currently, "variety" is used either as an equivalent to subspecies, connoting geographic variation, or as a sub-category under subspecies, denoting a minor, often ecological, variant.

As previously noted, the rank of "variety" generally lacks explicit legal protection under endangered species statutes. Federal law and many state laws only protect infraspecific taxa at the rank of subspecies. Since "variety" has long used as a synonym of subspecies, varieties are listed in both Federal and state endangered species lists, but this listing may not legally be defensible. Taxonomists concerned with rare plant protection should seriously consider taking up the use of the rank "subspecies" in place of "variety," to ensure that rare or endemic plant taxa are legally protected.

Hybrids

Despite the assumption of the isolation concept of speciation, plants do hybridize. Such hybrids may be sterile F_1 plants, swarms of backcrossed hybrids, or populations which may develop into new species. Reticulate evolution is not uncommon in plants, which may complicate cladistic analysis. Hybrid species (notho-

species) are regarded as distinct evolutionary species (Barrington et al., 1989), although differing from "normal" species which originate by divergence.

Nomenclatural rules allow us to recognize hybrids in three ways. A hybrid may be given a unique specific epithet, using standard nomenclatural format; *Scirpus peckii* is an example. This name conveys no useful information whatsoever. Alternatively, a hybrid may be designated as a nothospecies by the use of an "×" preceding the specific epithet, as in *Prenanthes* ×*mainensis*. This format at least conveys the warning that the taxon is a hybrid. Best, a hybrid may be designated as a combination of the names of its progenitor species, as in *Carex crinita* × *C. gynandra*. The last method conveys the most information, and is therefore the method of choice, but is not preferred by some compliers of rare species lists (Johnson, 1988) since this method is often used for F_1 hybrids.

There are substantial biological problems with hybrids as named in regional floras and as listed in state endangered species lists; for most of these taxa, virtually no information is available. A hybrid name may represent a single collection of a sterile F_1 plant, a backcrossed population, a new species derived from hybridization, or simply a variant individual, clone, or population within a morphologically variable species (Snaydon, 1984).

Taxonomic research is critical to provide sufficient biological information to enable regulators to determine whether a hybrid taxon should be listed and protected. I will not get into the questions of criteria and priorities for listing at this point, but simply examine the issues of hybrids. Most hybrid taxa have been named based on phenetics, generally restricted to morphology.

Recent research within the maritime species of *Carex* sect. *Phacocystis* (Cayouette and Morisset, 1986; Standley, 1990) has shown that several species within this group are of hybrid origin, based on analysis of chromosomes and genetics, and has clarified that several named taxa are sporadic F_1 hybrids. The hybrid species may be treated as a nothospecies, including all of the F_2 backcrosses, or as a distinct species which excludes the backcrosses, each of which has been named. For example, *Carex recta* (*C. aquatilis* × *C. paleacea*) is listed by Massachusetts but is incorrectly listed as *C. salina* var. *kattegatensis* by Maine.

There are a number of hybrids included in the New England endangered species lists, although none of the state endangered

species definitions includes hybrids. Little or no biological information is available for any of these listed taxa, which include *Asplenium ×ebenoides* (known to be sterile), *Carex ×mainensis, Carex ×trichina, Scirpus peckii, Amelanchier nantucketensis,* and *Prenanthes ×mainensis.* We do not know whether any of these named hybrids are capable of sexual or asexual reproduction or whether their hybrid status has been proven or is merely hypothetical.

A second issue which may arise when dealing with hybridization in listed plant taxa concerns the application of the Biological Species Concept. Strict application of the BSC implies that "good" species do not hybridize with other taxa under normal circumstances. As pointed out previously, many plant taxa do occasionally hybridize in nature, and this behavior may be the source of new genetic combinations and new species. None of the New England rare species protection acts, nor the Federal Act, invokes the BSC in all of its rigor. Occasional hybridization, therefore, should not be a biological or legal issue which impedes listing of rare taxa.

TAXONOMIC AND NOMENCLATURAL PROBLEMS IN NEW ENGLAND ENDANGERED SPECIES LISTS

For this symposium, I have compiled the endangered species lists of all of the New England states and New York and included Federally listed species. This compilation was done for three families of angiosperms, the Cyperaceae, Rosaceae, and Asteraceae. Species of leptosporangiate ferns were also examined. The compiled list provided the name under which each taxon is listed, the states in which it is listed, and the name which is used for that taxon in recent floristic treatments for the region. Specifically, each name was checked in Gleason and Cronquist (1991), Fernald (1950), and Ogden (1981).

The majority of species listed present no taxonomic problems. Of the 320 names listed, almost 70% were listed by the same name, at the same rank, on the state lists and in the floras referenced. However, over 30% of the listed names were identified as having taxonomic or nomenclatural problems, including differences among state lists or between state lists and published floras in name, rank, or taxonomic status. In general, the problems in the New England flora are similar to those described by Johnson

(1988) for palms. Although there are fewer difficulties with poorly described genera here, major problems are posed by taxa below the species level and by hybrids in both the poorly-studied tropical palms and the comparatively well-known temperate flora.

Three classes of taxonomic problems are recognized in this analysis. The first problem is a change in name, at the same rank: the taxon is recognized as a distinct entity, but placed in a different genus, kept within the same genus under a different name, or kept within the same species under a different infraspecific epithet. The second class of problem is that of a change in rank, in which the taxon is recognized as a distinct entity but is considered by some authors to be a distinct species and by others to be a subspecies or variety. The final class is that of taxonomic distinctness, the classic "lumping or splitting" problem, in which some authors have recognized a group of populations as a distinct taxon at either the specific or infraspecific rank, while other authors have not found the group of populations to be sufficiently distinct to warrant recognition at any rank. The list was first analyzed by families, then by type of taxonomic problem.

Within the ferns, approximately 30% of the listed names present problems. These include name changes at the generic level, changes in rank, and synonymy. Several instances were noted of biological problems, including hybridization and apospory.

The genus *Carex* predominates in the Cyperaceae and accounts for 60% of the listed names of endangered taxa. Taxonomic problems in rare New England *Carex* were treated by Reznicek (1989) at the 1988 NEBC symposium, and account for only 28% of the problems within the family. Overall, 30% of the listed names in the Cyperaceae present difficulties; most problems are in synonymy and changes in rank. The family presents surprisingly few biological problems, with few hybrids and no known asexual species. The spikerushes (*Eleocharis*) present the greatest proportion of taxonomic problems, with 45% of the listed names for this genus in question.

The Rosaceae had the highest overall percentage of taxonomic problems, including 50% of the listed names. Most problems are identified as synonymy at the infraspecific level, or as changes in rank. These problems are complex, however, as most taxa which present difficulties have been treated as infraspecific taxa, as distinct species, or have been lumped with different species by different authors. Biological problems, particularly asexuality, are

frequent; for example, *Crataegus bicknellii* (endemic to Nantucket) may be a distinct species (Kruschke, 1965), a variety of *C. chrysocarpa* (Fernald, 1950), or an apomictic clone of *C. chrysocarpa* with no taxonomic rank (Gleason and Cronquist, 1991).

The Asteraceae was comparable to the Cyperaceae in the incidence of taxonomic problems, with approximately 30% of the listed names in question. The most common issues were generic shifts and synonymy at the infraspecific level. Asexual taxa are frequent, although hybrids were not. Interestingly, *Bidens* appears to have the highest incidence of taxonomic difficulty within the family. Thirteen names are listed (although one, *B. coronaria,* appears to be a typographic error), with seven identified as problematic. The *Bidens eatonii, B. heterodoxa,* and *B. hyperborea* complexes all appear to need good taxonomic work. This group also illustrates problems between state lists: Massachusetts and Maine protect *B. eatonii* (no variety listed), while Connecticut protects two varieties, *B. eatonii* var. *major* and *B. eatonii* var. *simulans* based on the classification in Fernald (1950).

TYPES OF TAXONOMIC PROBLEMS

Generic Shifts at Same Rank

Some problems in lists occur when species have been transferred from one genus to another by a taxonomist who determines that two genera are not distinct or who recognizes that a group of species formerly placed in one genus represents a distinct genus. This important taxonomic decision is made at the generic level using the same data and the same process as at the species level. This problem may also occur when a nomenclatural study reveals that an error has been made in the selection of a generic name, but it is relatively rare with only 6 occurrences among the 320 names listed.

However, some inconsistencies do occur between state lists and between rare species lists and published references. *Diplazium pycnocarpon,* listed in New Hampshire, is listed as *Athyrium pycnocarpon* in Connecticut, but is referred to as *Thelypteris pycnocarpon* in Gleason and Cronquist (1991). Here we have the same taxon, listed under different names in different states, and also differing from the name used in the most recent regional flora. The coastal plain pond sedge genus *Psilocarya* includes *P.*

nitens and *P. scirpoides,* both listed in New York, Massachusetts, Rhode Island, and Connecticut. This genus has been included in the beak-rush genus *Rhynchospora* according to recent taxonomic studies (Gleason and Cronquist, 1991).

As another example, *Aster ptarmicoides* is listed by New Hampshire, but is listed in Massachusetts and Connecticut as *Solidago ptarmicoides.* Cronquist (Gleason and Cronquist, 1991) agrees that this species is a goldenrod rather than an aster. In general, this taxonomic problem is not difficult for regulators to solve and may not require taxonomic study; the listing of the same taxon under different generic names may be solved simply by including all major synonyms in the endangered species list.

Change in Specific Epithet

In this second class of taxonomic problem, different lists or floras maintain the same taxon at the species level, but treat it under different names. Generally, this situation is the result of nomenclatural research which has shown an incorrect name used at some previous date and is not a common problem in endangered species listing, occurring at most six times (less than 2%) within the list compiled here. One example is provided in *Carex,* where *Carex walteriana* var. *brevis,* listed in Rhode Island, should be *C. striata* var. *brevis,* as listed in Massachusetts. The listing of frequently used synonyms would reduce this problem.

Change in Varietal/Subspecific Epithet

This problem is similar to the preceding two, but at the infraspecific level. I have included in this category changes in name which may be required when infraspecific taxa are transferred from varietal rank to that of subspecies. This problem is infrequent, occurring in less than 2% of the listed names. *Rosa acicularis* ssp. *sayi* is listed by New York and is the preferred usage in Gleason and Cronquist (1991). However, these authors note that, if treated as a variety, the correct name would be *Rosa acicularis* var. *bourgeauiana.* Massachusetts, New Hampshire and Vermont avoid the issue by listing *Rosa acicularis,* without mention of which, if any, of the infraspecific taxa are included. Similarly, *Prunus pumila* var. *susquehana,* listed in Rhode Island, is treated by Gleason and Cronquist as *Prunus pumila* var. *cuneata.*

The listing of major synonyms would enable users to determine that these names refer to the same taxon, with the same listed rank.

Changes in Rank

The second most common type of taxonomic problem, and a close tie for first place, is taxonomic change caused by a change in rank. The taxon is consistently recognized as distinct, but is placed by some authors at the infraspecific level and raised by others to the specific level. Eighteen occurrences of this problem were noted, for an average frequency of 6%. This problem is not a critical taxonomic one, unless it occurs in a state which does not legally protect varieties, and can easily be solved by including synonymy. Mayr (1982) and others have pointed out that the decision whether to call a taxon a species or subspecies is arbitrary. In phylogenetic systematics, all taxa of all ranks have the same evolutionary status, i.e., they are monophyletic units which have a shared apomorphy (Liden and Oxelman, 1989). Examples include *Carex woodii* (Connecticut) which is also recognized as *C. tetanica* var. *woodii*; *Eriophorum spissum* (Connecticut) and *Eriophorum vaginatum* var. *spissum* (Rhode Island, also in Cronquist); *Antennaria petaloidea* (Connecticut), treated as a variety (*Antennaria neglecta* var. *petaloidea*) by Cronquist; and *Tanacetum bipinnatum* ssp. *huronense* (Maine), treated as a separate species, *T. huronense,* by Cronquist (Gleason and Cronquist, 1991).

Lumping and/or Splitting

Most taxonomic problems in listings arise because of what is generally referred to as "lumping" or "splitting," that is, changes in which taxa are not maintained as distinct (lumping), or in which new segregate taxa are found to exist (splitting). These changed designations include the majority of taxonomic problems noted in the compiled regional lists and may include changes at the specific or infraspecific levels. I will not delve into the reasons for these taxonomic changes, except to note that whether the result of a taxonomic study is "lumping" or "splitting" depends on the methodology used in the taxonomic study, the amount of difference between taxa which the investigator considered significant, and the species concept used by the investigator.

At the rank of species, 16 occurrences of lumping or splitting were noted, accounting for 16% of all taxonomic problems. One example is provided by *Carex garberi* and *C. aurea.* Although several states (New York, New Hampshire, Vermont, Minnesota) consider *C. garberi* to be endangered, and a Federal Candidate species, Cronquist (Gleason and Cronquist, 1991) considers it a synonym of the widespread *C. aurea.* However, a recent study by Katz et al. (1988) provided evidence that these are distinct species based on a multivariate study of morphological characters and that the listing of *Carex garberi* is valid.

At the infraspecific rank, changed designations are the most common problem and are recorded for 31 of the 320 listed names. Taxa are recognized by some states or floras as distinct taxa at the varietal or subspecific level, but other treatments recognize no infraspecific variation. As examples, New York lists *Scleria reticularis* var. *pubescens,* while Rhode Island (in agreement with Cronquist) lists only *Scleria reticularis.* Several states list *Waldsteinia fragarioides* (Massachusetts, Maine, Connecticut, New Hampshire), although recent floras recognize this taxon to be a variety (var. *fragarioides*) distinct from the European variety. Maine and New York (in agreement with Cronquist) protect *Bidens hyperborea,* while Massachusetts lists only the segregate *B. hyperborea* ssp. *colpophila.*

Several instances were noted of species which are recognized in recent floras to include two or more infraspecific taxa, yet state endangered species lists include only the species, with no mention of the variety or subspecies. This oversight creates a dilemma for the user. For example, does Maine's *Prenanthes racemosa* refer only to the autonym *P. racemosa* var. *racemosa,* or does it also include the segregate *P. racemosa* var. *multiflora*? Massachusetts lists, enigmatically, "*Scleria pauciflora* (2 varieties)." Which two? Fernald (1950) lists *S. pauciflora* var. *caroliniana* and *S. pauciflora* var. *kansana,* but omits the autonym var. *pauciflora,* which must also exist. Cronquist (Gleason and Cronquist, 1991) does not recognize any infraspecific taxa.

Other examples are more complex and involve taxa which are variously treated as a distinct species, an infraspecific taxon, or lumped. These designations appear to occur most frequently in the Rosaceae, as shown by the following examples: *Potentilla pensylvanica* var. *pectinata* (Vermont), *P. pectinata* (Fernald, 1950), or *P. pensylvanica* var. *bipinnatifida* (Gleason and Cron-

quist, 1991); *Prunus gravesii* (Connecticut), *P. maritima* var. *gravesii* (Federal Candidate), and *P. maritima* (Cronquist).

RECOMMENDATIONS FOR POLICY COPING WITH TAXONOMIC CHANGE

Rare species managers or regulators are constantly faced with taxonomic change as a result of the steady production of new monographic treatments, checklists and floras. Perhaps "constantly" is an exaggeration, since the investigation of systematics of north-temperate taxa is proceeding rather slowly at present. Still, name changes and new taxa appear and must be dealt with if lists of endangered species are to remain up-to-date and accurate. Coping with this change and updating lists is a difficult and time-consuming task. Most of the New England states relied, in their original listings, on *The Synonymized Checklist of the Vascular Flora of the United States, Canada, and Greenland* (Kartesz and Kartesz, 1980). This list provides the most recently published accepted name for each taxon, i.e., the result of the most recent taxonomic hypothesis, and lists all taxa published prior to 1980.

The use of such a standardized list solves some problems by basing an endangered species list on a single reference, but fixes the list in time without provisions for change. Since taxonomy and classifications are subject to change based on new research, new methodologies and new frames of reference, an endangered species list needs to be able to accommodate change. As noted by Kartesz and Kartesz (1980), taxonomic revision is needed even in our region.

The simplest way to accommodate taxonomic change without requiring extensive amendment to endangered species lists would be to include all major synonyms in the list, particularly those used in *Gray's Manual of Botany* (Fernald, 1950), *The New Britton and Brown* (Gleason, 1952), *The Manual of Vascular Plants* (Gleason and Cronquist, 1991), and *The Flora of New England* (Seymour, 1982). This procedure would ensure that the endangered species list does not simply use the most recently published name for a taxon, but would incorporate all names in common use and allow for taxonomic changes. If a new flora or monograph were published which used a new name or new combination, the older name would be incorporated by reference. The U.S. Fish and

Wildlife Service does include major synonyms in the annually published "Endangered and Threatened Wildlife and Plants; Review of Plant Taxa for Listing as Endangered or Threatened Species," and provides a discussion of taxonomic issues in the published Determination of Endangered Status, which is the official agency action required to place a species on the Federal list. At the state level, however, considerations of synonymy are rarely included.

There is a real need for endangered species lists to be usable and accessible to academic, amateur and conservation botanists, not all of whom have access to Kartesz and Kartesz (1980). If the endangered species list provides only one name without synonyms, the average user may be stumped and the list will not be sufficiently flexible to accommodate changes. For example, if an avid amateur in New York identifies a plant using *Gray's Manual* as *Potentilla egedei* var. *groenlandica,* how is this botanist to know that the plant is listed as endangered, since the New York list refers to it as *Potentilla anserina* ssp. *pacifica*? In Maine, if a coastal sedge is identified as *Carex recta* by a botanist using the new Gleason and Cronquist Manual, how is this person to know that the plant is listed as endangered under the name of *Carex salina* var. *kattegatensis*? A list which provided synonymies would avoid such problems by enabling users to readily determine species identities.

The synonym problem is evident in the use of different names for the same taxon by different states. We have already discussed some of these which result from name changes at the generic or species level: *Athryium pycnocarpon* in Connecticut vs. *Diplazium pycnocarpon* in New Hampshire; *Carex striata* in Massachusetts vs. *Carex walteriana* in Rhode Island; *Eleocharis parviflora* in Maine and Vermont vs. *E. parviflora* var. *fernaldii* in Massachusetts. Without a thorough synonymy, it is difficult to collate the state lists and accurately determine how many taxa are listed as endangered in the region. In my examination of these lists, for the four families treated, I have found 320 names, but these probably represent only 290 taxa. Johnson (1988) proposed that *no* infraspecific taxa be listed, but that the species be listed if any infraspecific taxa were thought to be endangered. This option, in his opinion, would reduce the number of taxa to be listed and would avoid overstating the number of truly threatened species in cases of taxonomic uncertainty. There may be reason to adopt

this strategy with regard to the New England flora. To cite a previous example, consider *Bidens eatonii*: since the existence of distinct varieties is possible but not proven, simply listing the species will provide protection to all populations of this taxon.

One type of taxonomic change is that which results in combining two taxa into a single species, only one of which was previously listed. For example, *Solidago purshii* is listed by New Hampshire as a rare species, but it has recently been combined with the more common *S. uliginosa* (Gleason and Cronquist, 1991). How do endangered species program managers make the decision whether to drop *Solidago purshii* from listing?

A second type of taxonomic changes is the change in rank, for example, in which a taxon previously listed as endangered at the species rank is reduced to a variety of a non-listed species. *Petasites palmatus* has recently been reduced to a variety of the widespread *P. frigidus* var. *palmatus*. An amendment to the list, or provision of synonymy, should solve this problem—unless the state in question has a statute which does not include taxa at the varietal level.

Endangered species program managers need strategies for updating lists and evaluating taxonomic changes. Most programs and lists reflect the names used in Kartesz and Kartesz (1980), which are the most recently published names of taxa, thereby assuming that the most recently published name is correct, an assumption that may present problems. Taxonomists aren't always right: evidence may not be adequate, evaluation may be flawed or methods may not have been applied correctly. Simply because a name has been published does not necessarily mean that it is closer to the "truth" than previous taxonomic treatments. The taxonomist may not know the group well, may not have studied the problem over the entire range of the group or may have used only local evidence or only herbarium material. In practice, published taxonomic changes are carefully considered and evaluated by the scientific community and either adopted or ignored, depending on the quality of the evidence presented in the original publication, a practice which may require several years before a name or rank change is fully accepted.

Each name change needs to be evaluated on a case-by-case basis before adoption. Since endangered species program managers do not have the time to do this and frequently lack expertise among their staff and interns, I suggest that each state develop a panel

of taxonomic experts which is responsible for keeping up with and evaluating nomenclatural and taxonomic changes. Each proposed change should be examined with regard to types of data used, methods used to interpret and analyze data, knowledge and expertise of the taxonomist, use of natural populations vs. herbarium collections, and systematic concepts used by the taxonomist.

Programs need to have in place a method for regular updating of lists. In some states, this updating will be as simple as publishing a revised list annually and ensuring that the program budget can support such a publication. In other states, rare species list revision will require publication of a draft for public review prior to official listing; this review carries certain dangers and subjects all listed taxa to comment and perhaps challenge.

Endangered species program managers and scientists need to increase interactions. Program managers need to understand scientific perspectives on rare species taxonomy and systematics, just as scientists need to understand the objectives and information requirements of endangered species protection. Systematics and ecologists can provide important information regarding criteria for listing as well as reproductive, genetic or autecological information necessary for the development of protection, restoration or management strategies. One contribution that the scientific community, perhaps via the New England Botanical Club, could make that would assist rare species managers would be to produce and maintain a data base of specialists in different plant groups.

INCREASING RESEARCH EFFORTS

Setting Research Priorities

Examination of endangered species lists reveals a large number of taxonomic problems which require research to address either taxonomic or systematic issues. Endangered species program managers, or their scientific advisory panels, can be effective if they set research priorities. My assessment of endangered species lists has shown that the major taxonomic problems concerning New England's rare taxa can be divided into four categories:

1. Does the taxon really exist as a distinct entity? Is this taxon,

whether ranked as a species, subspecies or variety, phenetically and/or biologically distinct from other taxa with which it has been combined, or from which it may have recently been split? In essence, this category of research addresses the validity of taxonomic lumping or splitting, and is crucial to the development of a scientifically valid endangered species list.

2. At what taxonomic level should a taxon be recognized? If a taxon is distinct, but there is disagreement in the published literature as to its rank as a species, subspecies or variety, research is needed to clarify the taxonomic rank. In some states this research may not be as critical since the taxon may be protected regardless of rank. However, if a state's endangered species statute does not explicitly include the rank of variety, taxonomic rank may also be critical to a scientifically valid list.
3. Are listed hybrids valid taxa? Are these taxa sporadic, sterile F_1 hybrids of no real systematic or evolutionary value, or are these established populations of reproducing F_2 plants, or are they stabilized taxa of hybrid origin? These questions are also important in rare species protection. A list which is defensible should not include questionable taxa or sterile F_1 hybrids. Some state statutes do not allow rare species status to be extended to hybrids. If such hybrids are to be listed and protected, it is important to understand their origins, genetics and reproductive potential.
4. What taxonomic groups need study? Based on my survey of the state lists, I can make some suggestions for research efforts that would be valuable for rare species listing and management, dealing with all three of these research goals. Groups or taxa which need taxonomic or biosystematic study include, but are certainly not limited to the following: the *Carex brevior/molesta/merritt-fernaldii* complex; *Carex katahdinensis*; *Eleocharis,* particularly *Eleocharis engelmanii/ovata* and *Eleocharis pauciflora/E. pauciflora* var. *fernaldii*; *Potentilla pensylvanica/pectinata*; *Prunus pumila* complex; *Amelanchier sanguinea/humilis*; *Artemisia campestris*; *Bidens eatonii, Bidens heterodoxa* and *Bidens hyperborea*; *Carex* × *mainensis* and *C.* × *trichina*; *Scirpus peckii*; *Prenanthes,* especially *Prenanthes* × *mainensis.*

Research Methodologies

Once research priorities have been established, endangered species program managers would need to determine the appropriate research methodologies to answer the questions needed. In general, taxonomic research needs to be carried out using as many methods as possible to ensure that all appropriate data are collected and analyzed. Studies should include use of herbarium material and natural populations; data should be collected on morphology, anatomy, cytology and genetics; data should be analyzed using both intuitive and computer-assisted techniques. Studies of breeding systems and reproduction may be appropriate to answer systematic and management questions. Finally, I would suggest that a study should include the entire complex over its entire geographic range in order to provide valid answers. Taxonomic studies which include only the taxa, or populations, contained within a single state are unlikely to provide the information needed to evaluate the status or rank of a taxon. The majority of taxa listed as endangered in New England are more widely distributed taxa at the limits of their range, rather than local endemics.

Examination of the biosystematic literature shows that north-temperate species, particularly rare taxa, are understudied despite opinions to the contrary. We have little or no data on genetic variation, the kind and extent of differences between related taxa, population structure, factors which contribute to rarity, reproductive biology, or evolutionary relationships for the majority of taxa. All of this information is needed to develop strategies that are effective in protecting and managing rare plant species (Bramwell, 1984). Too often our knowledge of rare species is limited to information available on herbarium sheets; there are some counterexamples, but these are infrequent. Pleasants and Wendel (1989) determined the evolutionary relationships and reproductive biology of the rare *Erythronium propullans* using genetic studies. One useful result was the discovery that this rare species consists of several widespread clones. Standley and Dudley (1991) determined the extent and pattern of genetic variation in the rare sedge, *Carex polymorpha,* and elucidated the relationship between canopy and population vigor. Based on this information, managers can target populations for protection and develop ecological management strategies. Other examples are few, and a reader is

struck by the gaps in our knowledge of rare plant biology. Biosystematic research can provide the knowledge of biology, evolutionary history and demographic patterns needed in order to understand the causes and consequences of rarity (Fiedler, 1986).

A more general research priority for New England might be to produce the kind of comprehensive biological treatment of rare taxa that has been produced for Minnesota (Coffin and Pfannmuller, 1988) or Canada (Argus and Pryer, 1990). Both volumes provide a full synonymy for each listed species and examine its status in other states. The Minnesota volume in addition provides detailed information on the ecology, distribution and biology of each species, with references to all published literature. Such a volume would be tremendously valuable in New England and would require that at least a minimal amount of taxonomic/biosystematic research be performed for each listed species.

Funding Research

Basic taxonomic or biosystematic studies of north-temperate species, focussing on problems at or below the species level, are not a priority for federal grant funding. State research funds are often limited or unavailable due to the local economy. However, such research costs money for supplies (genetic studies require costly chemicals), travel, computer time, student assistance, greenhouse space and postage for herbarium loans. A thorough taxonomic study of a species complex could require at least ten thousand dollars in research funds and would take at least two years. I have probably been optimistic on both counts. State and federal endangered species programs need to provide funds for systematic research and need to carefully assess their research needs and priorities if they are to produce rare species lists which will withstand legal challenge and adequately protect taxa by enabling all users to readily identify listed taxa.

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VANASSE HANGEN BRUSTLIN, INC.
101 WALNUT STREET
P.O. BOX 9151
WATERTOWN, MA 02272-9151

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SETTING PRIORITIES FOR REGIONAL PLANT CONSERVATION PROGRAMS

KENT E. HOLSINGER

ABSTRACT

Because plant conservationists have such an enormous task facing them, criteria for setting conservation priorities must be developed. In this paper I suggest a set of criteria for determining species conservation priorities based on three independent factors: (1) likelihood of persistence, (2) taxonomic distinctiveness, and (3) potential economic or ecological importance. Species with the highest priority for conservation will be those that are unlikely to persist without intervention, are taxonomically distinct and are economically or ecologically important. There are also a set of practical criteria that must be considered in setting priorities: What are the chances that the proposed conservation program will succeed? Could the program endanger existing natural populations? How expensive will the effort be? Regional plant conservation programs have something important to offer. Just as it makes sense to justify a regional plant conservation program for New England with reference to the distinctive characteristics of its flora, it makes sense to define regions within New England towards which our conservation programs are directed. Not only will regional plant conservation programs make a significant contribution to conserving our natural heritage, but their development will lead to new insights that can be applied to conservation on a much broader scale.

Key Words: Rarity, endangered species, conservation, conservation priorities, *ex situ* conservation, integrated conservation strategies

INTRODUCTION

The magnitude of the task facing plant conservationists on a global or national scale has been widely recognized. Raven (1987) guessed that nearly one-quarter of the 250,000 species of vascular plants will go extinct before the middle of the next century. Of course, most of the species at risk are found in the tropics, but the task facing conservationists in the temperate zone is also frightening, even on a local or regional scale. In Connecticut, for example, nearly one-fifth of the roughly 1600 native species of plants are endangered or threatened on a statewide level or are regarded as species of special concern. For 117 of these species it may already be too late; they are now known only from herbarium records (Mehrhoff, pers. comm.). The situation is similar throughout New England. In fact, there are so many species in imminent danger of extinction that we must make difficult choices

as we design a program for plant conservation in New England. Some species will be objects of concern early in this program's life, but others must wait. How do we make these choices? What criteria are appropriate for setting priorities? How do we tell when one species is a better choice for our efforts than another?

SETTING CONSERVATION PRIORITIES

To develop criteria for setting conservation priorities we must first decide what it is we are trying to conserve and why we are trying to conserve it. To accomplish this task we must recognize that conservation efforts can be directed either toward the conservation of species, especially rare and endangered ones, or toward conservation of the functional and structural attributes of important ecosystems. These aspects of conservation are often complementary, but they need not be. Plant species that are regarded as high conservation priorities are sometimes found in habitats that are otherwise unremarkable. Protecting the habitat for Furbish's lousewort (*Pedicularis furbishiae*), for example, also protected a unique and valuable watershed, but protecting the habitat for Texas wild rice (*Zizania texana*) will involve nothing more than protecting a drainage ditch near San Marcos, Texas. Furthermore, managing the dynamics of common species is likely to be more important in maintaining the structure and function of a distinctive ecosystem than is protecting the rare species within it.

Thus, the first task facing any conservation program is to define its mission, to decide whether it is directed at saving threatened and endangered species or at conserving examples of unique habitats and ecosystems. Although I focus on plant species conservation in this paper, we must remember that species conservation is only part of the story. Protecting and conserving significant ecosystems deserves an equal emphasis, even if the ecosystems involved have few high priority species. More importantly, the criteria appropriate for setting priorities in ecosystem conservation are likely to differ from those I develop here (Daniels et al., 1991).

Likelihood of Persistence

One criterion for setting priorities is obvious. Since we are concerned with conserving species, i.e., preventing their extinc-

tion, those species that are most likely to go extinct deserve higher priority than those that are less threatened. The problem, of course, rests in determining how likely extinction is. The International Union for the Conservation of Nature (IUCN) uses five categories to reflect the degree of threat: Extinct, Endangered, Vulnerable, Rare, and Indeterminate (IUCN, 1988). The Nature Conservancy uses a numerical scale from 1 to 5, ranking species separately at the global, national, and subnational levels (Nature Conservancy, 1988; Master, 1991). Both schemes combine qualitative judgments about the threat to populations with data on the number of separate occurrences. Similarly, legal protection is often based on qualitative assessments about the threat to populations and the number of occurrences.

In Connecticut, for example, three categories are recognized under the state's endangered species law (1989). An endangered species is "in danger of extirpation throughout all or a significant portion of its range within the state . . . and [has] no more than five occurrences in the state. . . ." A threatened species is "likely to become an endangered species within the foreseeable future . . . and [has] no more than nine occurrences in the state. . . ." A species of special concern has "a naturally restricted range of habitat in the state, [is] at a low population level, [is] in such high demand by man that its unregulated taking would be detrimental to the conservation of its populations, or has been extirpated from the state."

Mace and Lande (1990) criticized the IUCN system because they think its categories are excessively subjective. Their criticism would apply equally well to most other systems. How are we to assess the "danger of extirpation"? How long is "the foreseeable future"? How can we tell when human demand for a species is "detrimental to the conservation of its populations"? Mace and Lande propose a new system of threat categories (Extinct, Critical, Endangered, and Vulnerable) defined in terms of explicit probabilities of extinction over a specified period (Table 1). To assess such probabilities accurately would require a formal population viability analysis, incorporating information from demography, genetics, and metapopulation dynamics (Shaffer, 1981; Gilpin and Soulé, 1986; Belovsky, 1987; Menges, 1990, 1991; Murphy et al., 1990; Shaffer, 1990). Since the data necessary for detailed population viability analyses will not be available for many species, they also propose a set of criteria that can be used to assign a

Table 1. Mace and Lande's classification of the threats species face (Mace and Lande, 1990).

Classification	Likelihood of Persistence
Extinct	Zero
Critical	50% probability of extinction within 5 years or 2 generations, whichever is longer
Endangered	20% probability of extinction within 20 years or 10 generations, whichever is longer
Vulnerable	10% probability of extinction within 100 years

species to its proper category without a formal population viability analysis.

This new system represents a significant conceptual advance over existing ones, integrating as it does the theory of population viability analysis with the practical problem of assigning species to categories of endangerment. Unfortunately, as Master (1991) pointed out, the data needed to decide when the objective criteria are met are not available for most species, and the qualitative criteria that can be assessed require the same degree of subjective judgment as current systems. For practical purposes it is reasonable to accept Mace and Lande's conceptualization of the categories, but we will continue to use subjective judgments about the degree of threat facing a particular species and data on its distribution in assessing the likelihood of persistence for the foreseeable future.

Taxonomic Distinctiveness

Although the degree of endangerment is obviously an important criterion in deciding which species to protect, it is not the only criterion we should use. There are several plant taxa in which the entire world's population consists of one or a few individuals, and in at least some of these cases extensive efforts to conserve them seem misplaced. Grave's Beach Plum (*Prunus maritima* var. *gravesii*), for example, is known from only a single individual plant growing on the Connecticut shore in the town of Groton. Despite intense collecting throughout coastal New England in the century since it was first described, no other plants have been collected. It appears to be a mutant individual of the common beach plum that has never existed as a self-reproducing popula-

tion (Anderson, 1980). Similarly, *Betula murryana* is a fertile octoploid that combines the genomes of *B. allegheniensis* and *B. ×purpusii*. Since the only two trees known grow near their presumed parents, it seems likely that these are the only ones that have ever existed (Barnes and Dancik, 1988). Preserving cuttings of these taxa for horticultural or educational purposes may be worthwhile, but it seems obvious that conserving them is less important than conserving taxa whose populations have been severely reduced or threatened by human activities (Holsinger and Gottlieb, 1991).

Hybrids that are self-reproducing or species that are of hybrid origin, on the other hand, are worthy of protection, especially when they have acquired new and distinctive features. The sunflower relative *Helianthus paradoxus,* for example, is a stabilized hybrid derivative of *H. petiolaris* and the common sunflower *H. annuus*. It has diverged from its parents in flowering time, secondary compound composition, leaf and phyllary shape, and the habitat in which it is found (Rieseberg, 1991). Whatever its origin, its distinctive characteristics mark it as a new species, and it is clearly worthy of the same degree of attention that any other rare sunflower would receive. Similarly, *Aster ×blakei* is a stabilized hybrid derivative of *A. nemoralis* and *A. acuminatus* (Pike, 1970). Its habitat, typically the edges of bogs, the shores of ponds, and the swampy border of woods, is intermediate between that of its parents (Brouillet and Simon, 1981), and it is intermediate in many morphological traits. Nonetheless, it reproduces vigorously by rhizomes and is often found growing without one or both parents. Clearly it is behaving as a distinct species and deserves the same attention that we would give to any other rare *Aster*.

These considerations suggest a second important criterion to be used in setting conservation priorities. Taxa that are taxonomically more distinctive deserve a higher priority than those that are less distinctive. Why? Because our objective in conserving species is to conserve as much of the remaining biological diversity as we can, and a taxon that plays a unique ecological role or that represents a unique evolutionary line contributes more to that diversity than does one that is just another variation on the same theme. This assumption is not to suggest that less distinctive taxa are unworthy of protection or unimportant. After all, it is not just the beauty of his themes but the brilliance of his variations that makes listening to Mozart such a wonderful experience. But

think how much poorer the world would be if there were no Bach or Brahms, no Vivaldi or Puccini, no Debussy or Ravel. Similarly, the variety of sedges makes them a fascinating group, but to allow their variety to distract us from such distinctive species as Lizard's tail (*Saururus cernuus*) or Arethusa (*Arethusa bulbosa*) would be a grave mistake.

Taxonomic distinctiveness is probably the simplest and most accessible index of evolutionary and ecological uniqueness. Thus, we can use it as a guide in setting priorities. As a rule of thumb, I suggest that species in monotypic genera deserve greater attention than species in large genera, distinctive species deserve more attention than cryptic ones, and species deserve more attention than subspecies or varieties. Of course taxonomic judgments are notoriously variable from one group of plants to another, so this criterion must be applied cautiously. Within any particular group, however, taxonomic decisions tend to be made consistently, and taxonomic rank will quickly reveal when one taxon is more distinctive than another. In California about one-quarter of the taxa listed under the state's endangered species law are subspecies or varieties, suggesting that attention to minor categories has shifted the focus away from more important taxa (Holsinger and Gottlieb, 1991).

Economic or Ecological Importance

One reason we are trying to conserve biological diversity is that human beings may derive important benefits from it. Yields of major agricultural crops like corn, wheat, soybeans, tomatoes and potatoes have doubled or tripled in the last fifty years, for example, and nearly half this improvement is attributable to the use of genetic variation found in wild relatives of these crops (OTA, 1987). Use of these genetic resources has so far been limited by the need for reproductive compatibility between cultivated and wild species, but recent advances in molecular biology and genetics may make it possible to move genes coding for agronomically important traits into cultivated species from wild relatives that could not be included in a traditional crossing program. Similarly, the importance of plant products in the world's medicine chest is widely known. Nearly one-quarter of all prescriptions dispensed from community pharmacies in the United States contain active principles extracted from higher plants (Farnsworth and Morris, 1976). Taxol from the Pacific yew (*Taxus*

brevifolia) and vincristine/vinblastine from the rosy periwinkle (*Catharanthus roseus*) are merely two recent examples. Thus, another important criterion in determining conservation priority concerns the potential direct benefits that we may derive from plant species. Those species economically important themselves or relatives of economically important plants deserve a higher priority than those that are not.

To limit our considerations of human benefit from plant species to the direct benefit that may be gained from their use would, of course, be too narrow a view. We derive enormous indirect benefits from the role that plants play in maintaining the structure and function of important ecosystems. Rare species, which are the primary focus of this paper, may play a less important role in maintaining that function than those that are common, but they can serve as indicators of a system under stress. Loss of rare species may alert us to the loss of a unique and valuable habitat. Development on coastal sand plains in Connecticut, for example, is reflected in the declining numbers of False beach-heather (*Hudsonia tomentosa*), just as loss of sphagnum bogs has led to decline of Arethusa (*Arethusa bulbosa*). Loss of rare species might also be the first sign of change in ecosystem structure. Thus, it is reasonable to accord ecologically important species a higher priority for conservation purposes than those that are less important.

Special Considerations for *ex situ* Conservation Programs

For conservation programs like the national collection of the Center for Plant Conservation or the regional collection being developed as part of the New England Plant Conservation Program, there are additional considerations that must come into play. These programs aim to provide an insurance policy against catastrophes that would eliminate or endanger existing natural populations by establishing off-site collections of imperiled species. For temperate zone plants the method of choice for off-site preservation is long-term storage in seed banks, though maintenance of living collections may be an option for some long-lived plants (Holsinger and Gottlieb, 1991). The *ex situ* component of conservation programs must focus on species in which it can contribute significantly to the integrated conservation effort (Falk, 1987). It would be an unconscionable waste of limited resources to spend our time and money on species for which the prospects of *ex situ* conservation are limited.

I have already alluded to one important criterion for determining conservation priority in the *ex situ* component of a program, namely, the ability to store the species long-term as seed. Many temperate zone plants, especially those whose seeds are resistant to drying, can easily tolerate long-term storage at subfreezing temperatures if the seed is properly dried (Eberhart et al., 1991). Although meristem culture and other forms of tissue storage show some potential, expense and expertise necessary for such programs will make them impractical for all except the most important species. Species with recalcitrant seed, e.g., orchids and many aquatics, pose a real problem for *ex situ* conservation programs. It may be useful to include such species for horticultural, educational or research purposes, but only rarely can we justify the effort necessary to use living collections of short-lived species for conserving genetic diversity off-site. The amount of expertise and labor required simply make it impractical to consider more than one or two of the most important species for such an effort (Holsinger and Gottlieb, 1991).

Another important criterion is that no *ex situ* conservation plan should be considered for a species in which the collections necessary to ensure its success would seriously endanger remaining natural populations. After all, the whole purpose of the *ex situ* part of a program is to ensure the species' survival *in the wild.* Conservation of existing natural populations is the surest way to prevent loss of the genetic diversity necessary for long-term persistence. There may be rare cases similar to that of the California condor in which the only chance for a species' survival is to increase its population size through an off-site breeding program, but such programs should be considered *only* as a last resort. The record of ecological transplant experiments shows that the chances of successful establishment are very small, even when we try to match the ecological characteristics of source and destination populations as closely as possible (Huenneke, 1991). This outcome is particularly important to remember when development threatens a natural population. We should consider establishing a new population for mitigation only if the alternative is extinction.

Some Conclusions

I suggest that the conservation priority which a particular species receives should be based on: (1) its likelihood of persistence,

(2) its ecological or evolutionary distinctiveness as evidenced by its taxonomic distinctiveness, and (3) its ecological or economic importance. For programs that include an *ex situ* component we must also decide how likely *ex situ* efforts are to succeed for the species in question. Indeed, for any conservation program there is another layer of criteria that must be considered: How expensive will the effort be to conserve this species? What are the chances of success? Answers to these questions are obviously critical to the implementation of any program, but it is important that we distinguish between two questions that must be answered: (1) Which species should be the highest priority targets for a conservation program? (2) For which of these species are conservation efforts most likely to be rewarded? I shall focus only on the answer to the first of these, since it is that question which the three criteria I suggested above can answer.

Perhaps the most important thing to recognize about these criteria is that they are largely independent of one another. A species that faces a grave threat to its existence, for example, need not be particularly distinctive taxonomically nor particularly important ecologically. Obviously the highest priority should be accorded to those species that score high on each scale, but how are we to resolve conflicts among the scales? Does a taxon that is taxonomically distinctive but found in relatively stable populations deserve a lower priority than one that is less distinctive but whose populations are in imminent danger, for example?

Though I doubt that any general answer to these conflicts can be given, a rough priority scheme that ranks individual species in terms of their characteristics on three scales of measurement may be useful (Table 2). The priority scale I propose is divided into four categories: Very High, High, Medium, and Low. Species in the Very High category rank high on each of the three scales for conservation priority; those in the High category rank high on two; those in the Medium category in one; and those in the Low category rank low on every scale. Although the scheme presented in Table 2 treats each scale as a simple dichotomous variable, this treatment is done only to simplify the presentation. Likelihood of persistence, taxonomic distinctiveness and ecological or economic importance are all qualities that come in degrees, not absolutes. Thus, the categories suggested should also be regarded as points in a continuum, not as truly distinct categories.

The idea behind this scheme is a simple one: those species

Table 2. A scheme for setting conservation priorities.

Degree of Threat	Existing Populations Unlikely to Persist		Existing Populations Likely to Persist	
Taxonomic Distinctiveness	Very Distinct	Marginally Distinct	Very Distinct	Marginally Distinct
Ecological or Economic Importance				
Very important, good indicator species or close relative of economically important species	Very high priority	High priority	High priority	Medium priority
Less important, not a good indicator species and not a close relative of an economically important species	High priority	Medium priority	Medium priority	Low priority

deserving the highest priority for conservation efforts are those that are the most important in several different ways. Given a choice between a species that is both ecologically significant and taxonomically distinctive and another that is more immediately threatened but less significant ecologically and less distinct taxonomically, the first is a better candidate for conservation efforts, *all other things being equal.* Of course, all other things are rarely equal. This scheme and more elaborate ones, like the one proposed by Daniels (Daniels et al., 1991) which try to combine several measures of conservation priority must not be regarded as providing rigid rules for setting conservation priorities. Their usefulness, if they have any at all, comes primarily from their ability to clarify our thinking. They help us make sure that *all* aspects of the problem have been considered, but ultimately each case must be decided on its own merits.

APPLYING THE CRITERIA ON A REGIONAL SCALE

The first problem any regionally based plant conservation program must face is that of justifying its existence. For us the problem can be stated more specifically. Why should there be any efforts in New England at all when the number of species at risk pales in comparison with the tropics? Why should we regard

elements of the New England flora as imperiled when the species that are considered rare here often occur throughout the area? The small whorled pogonia (*Isotria medeoloides*), for example, is extant in every New England state except Vermont, where it is known historically, and herbarium records exist from as far south as Georgia. In California, on the other hand, rare species are often found in only one or two populations covering only a few acres. The serpentine endemics *Layia discoidea* and *Streptanthus niger,* for example, are each found in only two or three populations in a small geographic area. There are at least three reasons why a plant conservation program is necessary in New England despite these questions.

First, the groups that are at risk in New England are often very different from those that are imperiled in California, Hawaii, Texas and Florida, the states with the highest concentration of plants on the Federal endangered species list. Our global concern for conserving biodiversity requires that we direct some attention to areas like New England lest we lose important parts of our biological heritage. Second, the threat facing rare and endangered species in New England often may be a result of human-induced changes to their environment, while western endemics often appear to be recently evolved taxa that have never been more widespread. Fiedler (1987), for example, showed that rarity in Californian mariposa lilies (*Calochortus*) is a result of specific adaptations to habitats that are rare, while the rarity of running buffalo clover (*Trifolium stoloniferum*) apparently reflects the effects of European settlement (Bartgis, 1985; Campbell et al., 1988). Thus, rare western taxa have often shown their ability to cope with the ecological and genetic consequences of rarity, by the mere fact of their continued persistence (Huenneke et al., 1986; Holsinger and Gottlieb, 1991). Rare eastern taxa, on the other hand, may have become rare only after European occupation and may still be suffering from the effects of reduced population size and habitat fragmentation. Third, although endangered species are not necessarily important to the structure and function of distinctive ecosystems, they are sometimes good indicator species. Furbish's lousewort (*Pedicularis furbishiae*) is the most famous example in New England, but decline of Arethusa (*Arethusa bulbosa*) and False beach-heather (*Hudsonia tomentosa*) in Connecticut that I referred to earlier are two others.

Just as it makes sense to justify a plant conservation program in New England with reference to the distinctive characteristics

Table 3. A preliminary scheme of floristic regions in New England.

Coastal strand
Southern New England hardwood forest
Central New England transition forest
Northern New England mixed hardwood/coniferous forest
Northern New England coniferous forest

of its flora, it makes sense to define regions within New England toward which our conservation programs are directed. After all, rarity depends on the scale of observation (Harper, 1981; Rabinowitz, 1981; Kruckeberg and Rabinowitz, 1985). Side-oats grama-grass (*Bouteloua curtipendula*) is in no danger of extinction on a global scale; it is among the dominant grasses of the prairie in the central United States. In Connecticut, however, only a single population is known. Clearly, on that scale, it is a rare species. If our objective in designing a plant conservation program for New England is to preserve the diversity of its biological heritage, it behooves us to identify significant floristic regions or distinctive habitats within the area and to define rarity with reference to these regions. We should not define these regions too narrowly since we do not want to dilute our efforts, but defining them will help us to recognize rarities on a basis other than the artificial lines politicians have drawn. There are others far more qualified than I to suggest what these regions might be, but the scheme I suggest in Table 3 may serve as a basis on which to begin the discussion.

CONCLUSIONS

Many problems facing us as we design a program for plant conservation in New England are similar to those that have faced plant conservationists on a global or national level for years. The criteria I propose here, for example, are very similar to those developed by the Center for Plant Conservation for guiding the growth of its National Collection (CPC, 1991). It is not the criteria that are new, but the focus on a particular geographical region is new. This regional focus may allow us to accomplish two important tasks that more broadly based efforts have not. First, it helps us to knit together the sometimes competing objectives of species conservation and ecosystem conservation. At a global level, habitats of rare species may not be particularly significant, but at a regional level rare species often serve as indicators of

unique and valuable habitats. Second, it helps us build the case for programs that are directed toward conservation of genetic diversity within widespread species. Rare and endangered species are a legitimate focus for many conservation efforts, but we must not forget that the evolutionary potential of common species may depend on the amount of genetic variation they can maintain (Millar and Libby, 1991), and it is common species rather than rare ones that have the most to lose by the fragmentation of natural habitat increasingly associated with land development in industrialized societies (Holsinger, 1992). Regional plant conservation programs, like the one being designed for New England, have much to offer. Not only will they make a significant contribution to conserving our biological heritage, but their development will lead to new insights which can be applied to conservation on a much broader scale.

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DEPARTMENT OF ECOLOGY AND EVOLUTIONARY
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UNIVERSITY OF CONNECTICUT
STORRS, CT 06269-3043

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HABITAT MANAGEMENT: A DECISION-MAKING PROCESS

STEVEN C. BUTTRICK

ABSTRACT

Land protection alone is not sufficient to accomplish *in situ* conservation objectives. Habitat management is required to help address most of the threats to rare plant populations and their habitats. The high cost of land protection can often be countered by focusing conservation activity on public land where land acquisition is not an issue. It is still necessary, though, to focus conservation resources on populations that will best contribute to the protection of the species. A range-wide approach using Heritage data to compare all existing occurrences is discussed. A management planning process is described for those populations that do become the focus of *in situ* efforts. This planning process includes the development of ecological models that describe the interaction among the species, its habitat and key ecological processes. These models aid in the development of site designs and the establishment of measurable conservation goals. The success of management actions at reaching these goals should be tracked in focused biological monitoring programs. This feedback mechanism enables land managers to reevaluate their ecological assumptions, conservation goals and management strategies.

Key Words: Habitat management, conservation planning, biological monitoring, models

INTRODUCTION

This paper was prepared to bring up issues and generate discussions that could lead to habitat management policies of use to the New England Plant Conservation Program (NEPCoP) and the entire conservation community. Habitat management is a rather all-encompassing topic ranging from broad philosophical issues to detailed management procedures and planning. In attempting to narrow down the focus of this paper and produce something that may benefit most land or natural resource managers, I have chosen not to focus on details and techniques but rather on the management planning process. This paper discusses the role and importance of habitat management in the conservation of rare species and describes a process for management planning, implementation and measurement of results that could significantly contribute to regional plant conservation efforts.

LAND PROTECTION VS. HABITAT MANAGEMENT

This paper focuses on *in situ* species conservation: the preservation of viable populations in functioning habitats. In this context natural processes such as fire, hydrology, herbivory, wind, succession and competition need to be addressed when making conservation decisions. *In situ* conservation is accomplished through a combination of land protection (control of the land through legal interest, voluntary agreements, regulations or zoning) and habitat management.

Effective land protection has two critical components that need to be addressed whether the land is being protected for reintroductions or conservation of existing habitat and populations. The first component is site design: the identification and delineation of the land area needing some level of protection or protection consideration to ensure the security and defensibility of the targeted population. Site design decisions should be based strictly on ecological factors and not on ownership patterns. Proper site design cannot be done without an understanding of the natural processes acting on the habitat. Because our information is never complete, site designs should be reviewed and if necessary revised on a regular basis as more information becomes available. I use "site design" here rather than "preserve design" because of the connotation of land ownership that the term "preserve" seems to imply. A site is an area requiring protection planning, which can run from enforcement of existing regulations and zoning to voluntary protection, management agreements and outright conservation ownership. The role of site design in habitat management planning is further discussed later in this paper. The second component is protection planning: identifying the best protection strategy on a tract-by-tract basis (conservation ownership, where the fee is vested in some organization dedicated to conservation, is not always the intended goal or most appropriate level of protection for a parcel of land), and setting protection priorities (which tracts are most critical).

Habitat management has two components which I call "use management" and "biological management." Use management is aimed at controlling land use such as trail siting, visitor access and use, off-road-vehicle use and timber harvest. Biological management is aimed at controlling/reinstating/influencing the nat-

Table 1. Major threats to plant populations and their habitats.*

1. Direct habitat conversion (e.g., natural habitat to golf course, subdivision or mall)
2. Natural disturbances
3. Suppression of natural disturbances
4. Succession
5. Natural fluctuation in small populations
6. Introduction of exotic pests, diseases, animals, and plants
7. Imbalance in animal populations (e.g., deer)
8. Human caused changes in hydrologic regime
9. Inappropriate landuse and management (recreation, resource exploitation)

* Adapted from White and Bratton (1980).

ural processes (succession, competition, fire) affecting the population and its habitat.

Effective land protection requires careful consideration of site design and protection strategy (and successful implementation!). Effective habitat management requires a combination of biological management and use management. Long-term conservation of plant populations *in situ* will only be successful when land protection and habitat management are combined. Only the combined use of these two strategies can successfully address the major threats to plant populations and their habitats (Table 1).

Land protection alone is not an effective protection tool (White and Bratton, 1980). The act of setting aside land as a natural area does little to mitigate the effects of threats 3 through 9 in Table 1. A major reason for this lack of protection is that there are few "natural" areas in the true sense of the word (Falk, 1990). Human influence is felt throughout North America. Hunting policies have affected animal populations by eliminating predators and thereby increasing deer herds, for example; hydrologic cycles and ground water levels have been impacted; fires are not left to burn; forests are logged; exotic species dominate in many habitats; forests are dying from acid rain and are becoming increasingly fragmented; and the list goes on. Habitat management attempts to address the majority of the listed threats and should be considered a protection tool at least equal in importance to land protection. For *in situ* preservation, management is the only protection tool aimed directly at the resource we are trying to protect rather than just the land. However, protection of land is still a critically important protection tool for three reasons. First, creating a well-designed, legally protected natural area greatly decreases the threat of habitat

conversion, probably the greatest threat to natural diversity. The higher the level of protection, such as a state dedicated natural area, the more secure the reserve. Second, well-designed sites and protection strategies can also mitigate the threat from natural disturbance; for instance, small isolated patches of mature forest can be devastated by a single disturbance event. In 1990, a 40-acre old-growth white pine stand at the Conservancy's Cathedral Pines Preserve was shattered during a single severe windstorm (Lapin, 1991), whereas an old-growth forest at the Big Reed Forest Reserve in Maine is more buffered from a single storm event by its 5000 acres and its location in a forest matrix with a more moderate edge than the sharp boundary of agricultural land and development at Cathedral Pines. Finally, owning a natural area gives the owner the right to manage it. This combination of land protection and habitat management is the key to long-term protection. If, however, the resource is not the focus of management activity at the site, the advantage could be, and often is, lost.

MANAGEMENT ON PUBLIC LANDS

Data from the Natural Heritage Program Network have documented that in many states more than 50% of the occurrences of rare species and significant habitats are found on public lands. In 1991 Heritage programs in Connecticut, Massachusetts, Rhode Island and New Hampshire documented 461 sites of global ecological significance. It was estimated that 233 of these sites were completely or in part publicly owned. Public ownership includes federal lands owned by the US Forest Service, National Park Service and Fish and Wildlife Service, as well as lands owned by state agencies (state parks, wildlife management areas, state university lands, etc.) and local agencies such as counties and towns. We often consider these public lands to be "protected" when in fact most are not. While they often accomplish the land protection aspect of conservation, many of these areas do little if anything to assure the long-term preservation of specific populations. The Nature Conservancy does not consider a publicly owned site "protected" unless the management needs of the target species are specifically addressed in the site's management plan.

In 1991 less than one third of the 233 sites with public ownership were considered protected. For a number of reasons these sites are often not managed for the rare species found there or for

the maintenance of their habitats. The pressure for recreational use and the multiple use management priorities of many agencies often conflict with the management of rare plant populations (Falk, 1990). Often resources are not available to develop and implement management plans and very often the manager is simply not aware of the existence of rare species. This latter situation is being effectively addressed in some states by programs such as the Maine Critical Areas Program and the Massachusetts Natural Areas Registry designed to inform public land managers of the existence and significance of rare populations and provide management guidelines. The Vermont Nature Conservancy and the Vermont Natural Heritage Program have developed a registry program that provides maps and management guidelines for inclusion in the public agencies' land management plans. Many Natural Heritage Programs provide management information to public land managing agencies for rare species and exemplary natural communities in the state.

To address conflicting management priorities on public lands, New England conservation community should emphasize the need for programs aimed at: (1) assisting and guiding states in the development of natural area and endangered species legislation, (2) raising the existing levels of protection through special designations such as Special Interest Areas and Research Natural Areas, and (3) providing management information and assistance. Cooperative research efforts should be encouraged. For instance, in Massachusetts William Patterson of The University of Massachusetts is working with Miles Standish State Forest and the National Park Service on Cape Cod to demonstrate the effectiveness of prescribed burning in maintenance of pine-barren and scrub-oak communities and the reduction of fuel loads. Patterson and Peter Dunwiddie of Massachusetts Audubon, with the cooperation of The Nature Conservancy, are working with the National Park Service to evaluate potential effects of hands-off management on community diversity and rare species at the Cape Cod National Seashore.

The remaining populations occur on private lands, some protected by private conservation groups such as The Nature Conservancy, but many are not. Working under the assumption that most species are lost through ignorance rather than willful intent, registry and landowner contact programs have been established in many states to inform private landowners of the significance

Table 2. Plant population ranking criteria.

Quality	Representativeness of the population, especially as compared to element occurrence (EO) specifications, including maturity, size and numbers
Condition	How much the habitat and population itself have been damaged or altered from their optimal condition and character
Viability	Long-term prospects for continued existence of the population
Defensibility	Extent to which the population and its habitat can be protected from extrinsic human factors that might otherwise degrade or destroy it

of their property and occasionally to provide management information in terms of activities that should be avoided within the site, such as application of herbicides and mowing. A question that is often asked is how much protection and management effort should be expended on any particular unprotected population. Is the chance too great that the investment made in management and land protection will be lost? In general, conservation resources should be expended in proportion to the perceived importance of a particular population in contributing to the preservation of the species.

A RANGE-WIDE APPROACH TO PROTECTION PLANNING

Resources required for *in situ* conservation are substantial; one-time cost of land protection and start-up and long-term costs of management should be carefully weighed against the benefit of protecting a particular population and the chances of that population's long term survival at the site. This evaluation is best done by taking a range-wide approach to protection planning. A plan should be developed to protect the species (not just a population) by looking at and comparing all populations of the plant, or, in the case of regional or state rarity, looking at all the populations within that area. Taking a range-wide approach to protection planning allows the conservation community to make informed management and protection decisions for each population based on its quality, condition, viability and defensibility (Table 2). The Natural Heritage Program Network uses these parameters to as-

Table 3. Element global rank record.

Identifiers			
Name:	CAREX POLY-MORPHA	Common Name:	Variable Sedge
Description:	Plant, monocot, Cyperaceae		
Taxonomy:			
Global Element Occurrence (EO) and EO Ranking Specifications			
Habitat:	Primarily an upland species in dry, open woods, mostly acidic soil; frequently occurs in wetland ecotones and occasionally in sphagnaceous wetlands; also found in disturbed habitats such as those along railroad rights-of-way, sand pits, and cart roads; small wind dunes atop knobs in WV.		
Permanence:	Permanent.		
EO Specifications:	Any natural occurrence of one or more plants.		
A-Rank Specs:	A large population of plants covering 10 or more acres and containing tens of thousands of ramets, hundreds of fertile culms. Such a site, would have very little disturbance, and a lack of significant competition from exotic plant species.		
B-Rank Specs:	A moderate population of plants covering 5 to 10 acres and containing thousands of ramets, including many fertile culms. Such a site might have noticeable disturbance and/or moderate invasions by exotic species.		
C-Rank Specs:	A small population of plants covering 2 to 5 acres, or containing much less than a thousand ramets. Reproduction can be very poor, with few or no fertile culms present. Such a site might have significant disturbance, and/or significant invasions by exotic plant species.		
D-Rank Specs:	A population of plants covering less than 2 acres, or containing much less than a thousand ramets. Reproduction can be very poor, with few or no fertile culms present. Such a site would have a high occurrence of disturbance, and/or significant competition from exotic plant species.		
Element Global Ranking Criteria			
Estimated EOs:	C		
Est. EOs Comment:	Approximately 25 EOs altogether: CT—1; MA—1; ME—5; NH—1; NJ—2; PA—7; RI—1; VA—7–10; WV—5.		

Table 3. Continued.

Abundance:	
Abund. Comment:	Population size varies from one to several individuals at a site to 1000+ individuals at a site.
Range:	B
Range Comment:	Extant in CT, MA, ME, NH, NJ, PA, RI, VA, & WV. Historical records from DE, MD, NY. Some states with only one population.
Trend:	
Trend Comment:	Declining?/extirpated in all states except, perhaps, VA & WV.
Protected EOs:	B
Prot. EOs Comment:	Largest population in WV is protected, in part; one population in NJ is in a State Natural Area.
Threat:	
Threat Comment:	Very threatened in New England; populations in WV are under little imminent threat, yet seemingly remote rugged sites can be bulldozed and developed almost overnight. All sites, except preserve, are susceptible to recreational development for vacation homes on ridge tops.
Fragility:	B
Fragility Comment:	May require some disturbance to habitat to prevent succession to woody vegetation.
Other Considerations:	
Global Rank and Summary Reasons	
Global Rank:	G2 Global Rank Date: 90-06-22
Summary Reasons:	Loss of habitat, extirpated from 3 of 12 state range, many populations small and most are on privately-owned unprotected land. Four states with only one population each (CT, MA, NH, RI).
Global Action Recommendations	
Protection Needs:	Seek protection of several New England, as well as VA populations and other sites in WV.
Inventory Needs:	Seek extant population(s) in NY. Search appropriate habitat in New Jersey and Virginia for new populations.
Research Needs:	Research on effects of natural succession by woody vegetation, shading, and fire on reproduction and population vigor.

Table 3. Continued.

Stewardship Needs:			
Record Maintenance Responsibility: WVHP		Edition Author:	Russell, C. & P. J. Harmon
Edition Date:	91-09-05	Update Date:	91-10-22

sign an overall rank (A = Excellent, D = Poor) to each occurrence (for a plant, an occurrence can usually be defined as a population). Guidelines for ranking occurrences of a particular species are developed on a species by species basis and documented in an Element Global Ranking Form. This form also provides the basis for the development of an "element conservation priority rank" (Master, 1991). A global ranking form for *Carex polymorpha* is shown in Table 3. As the Heritage Network collects data for a species on an occurrence by occurrence basis, these data are used to further evaluate the naturalness or quality of the habitat, and the urgency for habitat management and protection actions (Table 4). Heritage Network data can be used to develop range-wide pictures or scorecards of the status of all populations of a species. An incomplete scorecard comparing 10 occurrences of *Carex polymorpha* is shown in Table 5. By comparing overall occurrence rank, land ownership patterns, protection status, population status and protection urgency, a population's importance in the overall protection of the species begins to emerge. Genetic data would be a valuable addition to this population by population evaluation.

With information generated by the Natural Heritage Program Network, there is now an opportunity to develop range-wide protection plans at the national, regional or state level. I would like to advocate the need for state or regional protection planning meetings. These meetings would have as an agenda protection of a number of species of concern within the state or region, and the specific goal of developing protection strategies and assigning next actions for each occurrence of each species. Participants should include those who are actively involved in direct conservation of the species, including representatives from federal and state management agencies who have occurrences of the species on their land. Formal Protection Planning Committees have been suc-

Table 4. Urgency ranks.

PROTECTION URGENCY

A protection action typically involves raising the current status (CS) of one or more tracts at the site. However, a protection action may also include activities such as working with public and private entities to minimize adverse impacts to element occurrences (EOs) dependent on particular water quality and hydrologic parameters at a site.

Threats that might possibly require a protection action include: 1) anthropogenic forces that threaten the existence of one or more EOs at the site (e.g., development that would destroy, degrade, or seriously compromise the long-term viability of an EO; timber/range/recreation/hydrologic management that is incompatible with an EO's existence); 2) inability to undertake a management action (*see* Management Urgency) in the absence of a protection action (e.g., obtaining a management agreement); 3) in extraordinary circumstances, a prospective change in ownership or management that will make future protection actions much more difficult.

P1: Immediately threatened by severely destructive forces (within 1 year of rank date)—now or never!
P2: Threat expected within 5 years
P3: Definable threat, but not in the next 5 years
P4: No threat known for foreseeable future
P5: Land protection complete

MANAGEMENT URGENCY

"Management action" includes both biological management (e.g., prescribed burning, exotic removal, mowing) and use management (e.g., barriers to prevent ORV abuse, patrol for collecting/hunting/trespass, trail rerouting).

M1: (a) New management action required immediately or population could be lost or irretrievably degraded within 1 year
(b) Ongoing annual management action must continue or population could be lost or irretrievably degraded within 1 year
M2: (a) New management action will be needed within 5 years to prevent loss of population
(b) Ongoing, recurring management action must continue within 5 years to prevent loss of population
M3: (a) New management action will be needed within 5 years to maintain current quality of population
(b) Ongoing, recurrent management must continue within 5 years to maintain current quality of population
M4: Although not currently threatened, management may be needed in the future to maintain current quality of population
M5: No serious management needs known or anticipated at site

Table 5. Scorecard for *Carex polymorpha* showing selected populations.*

Occurrence #	Site Design	Occurrence Rank	Protection Urgency/ Comments	Management Urgency/ Comments	Last Observed	Status	Ownership	Site Protection Status
CT-001	No	C/D	—	—	1990	100's of stems	Unknown	Unprotected
MA-001	No	C	P4	M3	1987	2 subpopulations 700–800 indiv.; about 60 fertile culms seen	Public/local; information incomplete	Public land registry
ME-004	Yes	A−	P1 Threatened with development	M3	1990	1000's of stems in scattered subpopulations	Multiple private tracts	Unprotected; town planners aware of occurrence
ME-007	No	D	P4 Inappropriate land use	M2 Succession	1990	More than 1000 plants, few fertile	Multiple private tracts	Unprotected
NH-002	No	A	—	—	1990	1989—about 1 million plants in immature fruit. May occur on one square mile of habitat	Unknown roadsides, disturbed habitat	Unprotected

Table 5. Continued.*

Occurrence #	Site Design	Occurrence Rank	Protection Urgency/ Comments	Management Urgency/ Comments	Last Observed	Status	Ownership	Site Protection Status
NJ-006	Yes	D	P1 Hydrologic threats; road maintenance	M2 Succession	1988	200+ individuals	Multiple private and public (local)	Most tracts registered—seek management agreements
PA-502	Yes	A	P1	M3	1990	5000–10,000 individuals; in # of local spots over 5600+ acres	Multiple private	Some registered, some TNC ownership, some unprotected
PA-513	Yes	B	P2 Inappropriate land use	M3 Succession; needs prescribed burning	1989	1001–10,000 individuals; excellent viability & defensibility	Public (federal)	Good intentions but unprotected
VA-011	Partial	D	P4	M4	1990	< 100 plants in restricted area by trail & spring	Public (federal)	Wilderness area, but not managed for *Carex*

Table 5. Continued.*

Occurrence #	Site Design	Occurrence Rank	Protection Urgency/ Comments	Management Urgency/ Comments	Last Observed	Status	Ownership	Site Protection Status
WV-002	Partial	A	P2	—	1981	> 1,000,000 stems in undisturbed habitat	Multiple private	Partly owned by TNC

* Data from State Natural Heritage Programs: CT Natural Diversity Database, MA Natural Heritage and Endangered Species Program, ME Natural Heritage Program, NH Natural Heritage Inventory, NJ Natural Heritage Program, PA Natural Diversity Inventory, VA Division of Natural Heritage and WV Natural Heritage Program.

cessful in a number of southern states (Pearsall, 1984). Informal, small protection planning meetings have been successful in our northeast region.

Protection planning meetings should focus on reviewing and evaluating the status of all occurrences, determining the appropriate needs and next actions for each occurrence (whether it be monitoring, active management or land protection), and assigning responsibilities for all actions. To be truly effective, these meetings should be held on a regularly scheduled basis so that progress toward accomplishing assigned actions (we should never underestimate the importance of peer pressure in getting things done) and the effects of those actions can be evaluated. Next, actions should be recorded in a networked database. The Nature Conservancy's Biological and Conservation Data system, used by the Natural Heritage Program Network and a number of federal agencies, can track actions and responsibilities and link these actions to individual species, populations and tracts of land.

PROTECTION PLANNING AT THE POPULATION LEVEL

When a decision is made to focus conservation resources on a particular site more information needs to be collected and another decision making process needs to be developed. Figure 1 outlines the recommended process for protecting and managing rare plant habitat. This process emphasizes the need to understand the dynamics of the species and its habitat and the processes that directly affect them, the need to carefully develop and articulate conservation goals, and the need to develop monitoring programs to track our success at meeting these goals in order to evaluate and modify our ecological and management assumptions.

THE ECOLOGICAL MODEL

The goal of *in situ* conservation is to protect the plant population in the context of the habitat in which it is found. We are not trying to create wildland gardens, where plants are carfully tended and seeds germinated and planted. Wildland gardening is often the result of a lack of information on how the biological system works.

A case in point is Peter's Mountain mallow, *Iliamna corei*

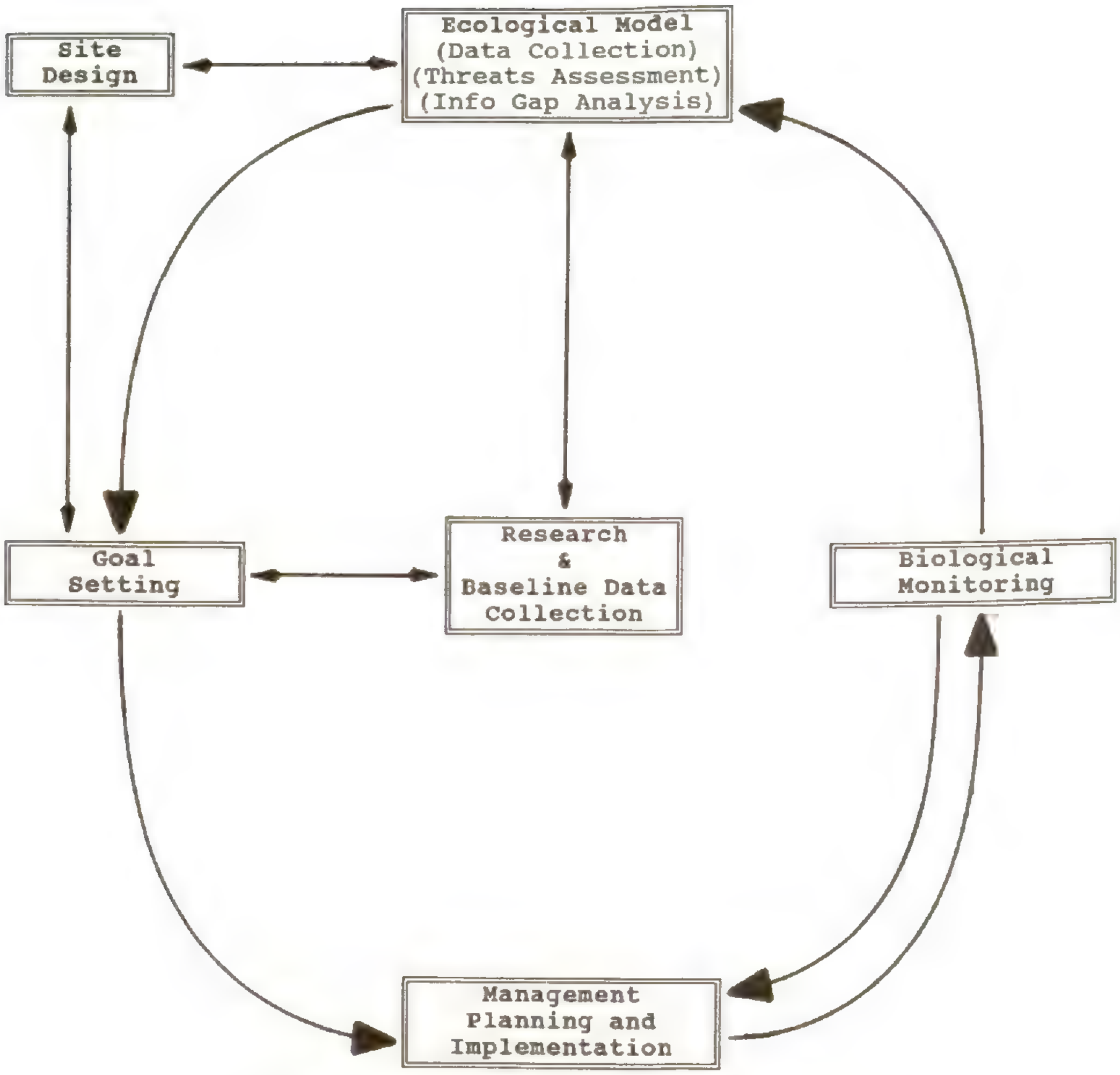


Figure 1. Habitat management planning process.

(Sherff) Sherff, known from only one site in southwestern Virginia (Williams et al., 1992). When this herbaceous perennial was discovered in 1927, there were approximately 50 individuals. In the 1960's and 1970's the population precipitously declined, and today there are only four individuals left at the site. There has been no recruitment in the population and there are now high levels of flower abortion and low levels of seed production. Management has been essentially wildland gardening focused on maintaining these last four plants, including caging to prevent deer browse, and watering during periods of drought. Seeds collected from the plants were scarified, germinated and grown at Virginia Polytechnic Institute and State University.

What was lacking in the above scenario was an understanding of how biotic and abiotic factors affected the growth and repro-

duction of the mallow. True *in situ* conservation (the preservation of viable populations in functioning habitats) requires an understanding of the life cycle of the species targeted for protection, the relationship between the species and its habitat, and the abiotic and biotic processes acting on both. It is the description of this dynamic relation that I am calling an ecological model. This model might be simple (and initially it will be) or, as our understanding of the system develops, complex. It can be qualitative or quantitative, textual or diagrammatic. Whatever form this model initially takes, it requires land managers to put down on paper their knowledge and assumptions on how the system operates. Regardless of complexity or completeness, the model must have two traits: it must be descriptive, showing our understanding and assumptions of how the system works, and it must be predictive.

To develop the model the land manager needs to collect all available information on the species, the population of interest and the site itself. If appropriate, information on more common but closely related species found in similar habitats can be collected to supplement available data on the rare plant (Baskin and Baskin, 1986). Information on the site and the population should emphasize disturbance and management history. A careful assessment of the threats listed in Table 1 should be made. Because our knowledge of the ecological dynamics within a system is never complete, the ecological model will never be complete and will only reflect the current state of our knowledge.

In the case of *Iliamna corei*, research initiated in 1986 by The Virginia Department of Agriculture and Consumer Services, the US Fish and Wildlife Service, the Nature Conservancy, Virginia Polytechnic Institute and State University, and recent work by Baskin and Baskin (1990) have found that the species is self-incompatible and cross pollination among the four plants is probably infrequent, that a large seedbank exists at the population, that seed germination is triggered by fire, and that plant growth is negatively affected by shading and neighboring vegetation (Williams et al., 1992). With this information, a model of how the system works begins to form (Figure 2) and leads us to ask further questions: What was the frequency and timing of fire in this habitat? Are there other unexpressed seedbanks? Management predictions can be made as to appropriately time prescribed burns

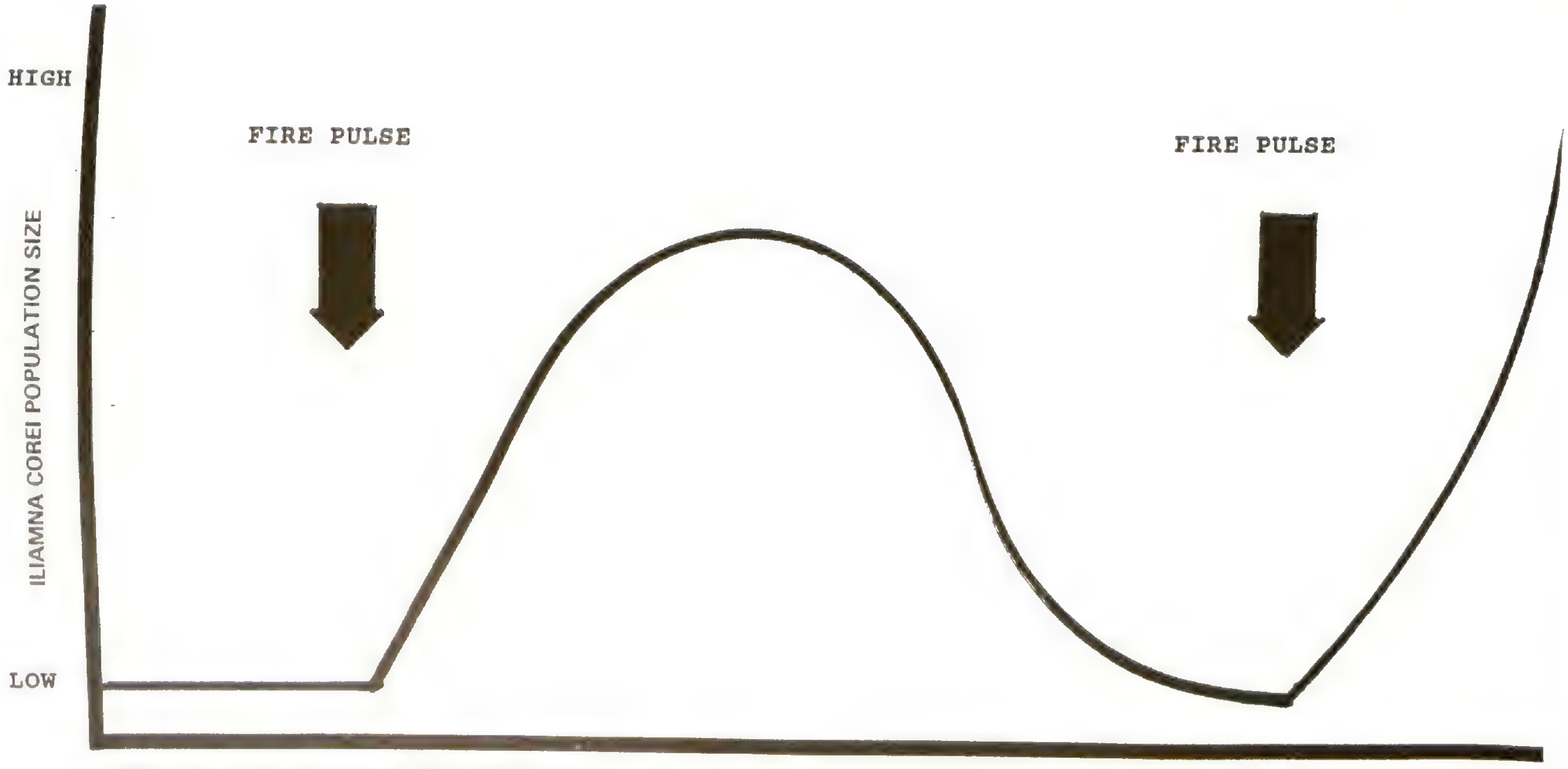
to stimulate the seed bank, and overstory thinning to promote development of individuals. Research is currently underway to determine the fire history of the habitat and a research proposal, developed by Caren Caljouw of the Virginia Division of Natural Heritage, has been funded to determine, on site, the effect of prescribed burning on added seed and the existing seed bank.

Development of the ecological model drives the rest of the protection planning process at a site (Figure 1). Specifically, the model should point out areas of weakness in the information base, and thus where research or baseline data are needed. Additionally, the more we know about the threats and needs of specific populations and their habitats as well as the biotic and abiotic processes affecting them, the better we are able to design preserves that will allow these processes to function and reduce identified threats. Similarly, this ecological model will guide management activities aimed at maintaining or reintroducing critical processes such as fire, flooding and herbivory, and at eliminating or reducing threats such as exotics, succession and negative land management practices.

Storage and management of both the sources of information used to develop the model, and the model itself, need to be carefully considered. The Biological and Conservation Data system's source, stewardship and species and community characterization datafiles provide not only a place and format for assembling and documenting this critical information but also a system for disseminating much of this information so that everyone interested in the conservation of a particular species can benefit from the accumulated knowledge of others and not end up reinventing the wheel.

SITE DESIGN

The ecological model should provide much of the information needed to develop a site design. A well-thought-out site design is probably the most critical step in the habitat management planning process; it minimizes the need for extensive interventionist management and maximizes the chances for conservation success. Without a well-designed site plan, fatal flaws in our ability to protect and manage the critical natural resources occurring at a site might not be detected until after a major investment of conservation time and money. A complete site design has three components. The first, which was mentioned at the beginning of this



Prepared by Dr. Charles Williams, Virginia Field Office, The Nature Conservancy

Figure 2. Conceptual model showing population dynamics in relation to fire and canopy closure.

paper, is the identification and delineation of the land area needing some level of protection or protection consideration to ensure the security and defensibility of the targeted population and its habitat, to moderate or eliminate threats, and to maintain or reinstate the natural processes needed to maintain or enhance the species and its habitat. While a single species often directs conservation attention to a particular site, we are usually protecting more than one endangered plant there. Most rare species do not occur in isolation and many occur within rare or exemplary communities. The design must take into account all resources to be protected at the site.

Site design must consider the major processes acting on the habitat. It needs to look at the habitat in relation to the larger landscape in which it occurs and evaluate current and potential activities within that landscape that could impact the resources we are trying to protect. In the case of a rare plant population in a coastal plain pond in southeastern Massachusetts, obvious visible threats to the system might include development along pondshores and inappropriate use such as all-terrain vehicles (ATV's). But these issues by themselves are not enough to consider in the site design. The maintenance of the coastal plain pond habitat is controlled by the hydrology of the region. A critical protection goal will have to be the maintenance of groundwater quality and quantity, a goal that needs to be addressed in the site design and cannot be resolved by land acquisition. Direction and speed of groundwater flow need to be determined to help evaluate potential threats from septic systems and to help calculate pondshore setbacks. Overall water quantity entering the site needs to be determined to limit quantity of groundwater removal by pumping at nearby municipal wells.

The needs of active management, such as prescribed burning, also must be considered in site design. The land area necessary to implement safe and effective prescribed burns and address smoke management issues must be taken into account. Plans for active management can be difficult or impossible to execute without a well-designed site.

The second component of a complete site design is a protection plan or strategy for the land. All of the above design work should have been accomplished without regard to ownership patterns. Now ownership information must be collected and appropriate

levels of protection, from fee ownership to simple landowner contact to zoning considerations, need to be identified. Finally, management issues need to be reviewed and an outline of management needs prepared. This work should all be done before any land protection work begins. The site design, then, should outline the scope and cost of the conservation activity needed at a particular site.

SETTING CONSERVATION GOALS

A critical step between development of the ecological model and development and implementation of a management program is establishment of conservation goals (Figure 1). The need for establishment of goals has been well articulated by Schroeder and Keller (1990). As managers of biological resources, we are constantly making decisions. Even the decision to do nothing, often called passive management, is a management plan with real consequences to ecological processes. This approach to habitat management planning requires us to state the potential management results that would reinforce our commitment to management strategies, and the results that would lead us to alter our ideas about how stewardship should proceed. Before implementing a management program, land managers must ask themselves what they are trying to accomplish through this management. Setting of these conservation goals needs be done early in the planning process to avoid misdirected management and wasted resources.

Conservation goals also need to be clear, concise and measurable. Generally, the goal for a rare plant population is to maintain or improve it. Goals stated this way are not useful because "maintain" and "improve" are undefined and not measurable. Quantifiable goals are not easy to develop and often require a level of information which we do not have, or they force managers to state assumptions that are unproven or of which they are unsure. We seldom have complete information concerning species life histories, dynamics of populations and communities, or environmental relationships. Additionally, each population is unique, making it difficult to extrapolate from available species information. In this case, however, uncertainty should not be a bar to action. By articulating our goals we enable our colleagues to examine our operating premises, and to critique them. We also help

assure continuity despite personnel changes. And most importantly, we can design and implement monitoring that will, over time, allow us to refine these goals and our site management plans. Goal setting should be viewed as a dynamic and flexible process and representative of our current understanding of the system.

Setting conservation goals requires four steps. The first step is the identification and selection of features or parameters that best indicate the health and status of a population and/or habitat. This goal might reference size of the population or size of the area occupied within a range over time; or the size (age) class distribution of a population. Frequency is often used, especially in the West (Smith et al., 1986). For *Carex polymorpha,* a clonal species, individuals can be counted but density needs to be better defined. Are we talking about density of ramets or genets? Our ecological model shows that as the canopy closes, flowering and seed set decrease (Standley and Dudley, 1991). A conservation goal based on number of ramets would not really represent the health of the population. Possibly an estimate of the number of ramets and percentage of these setting seed would be better indicators of the status of *Carex* at a site. If canopy cover is a factor, then a goal needs to be set for this parameter also.

The second step is to develop a baseline. To set a goal it is necessary to know the current status of the population and habitat in terms of the selected parameters. For parameters that are variable or fluctuate over time, such as density in an annual species, baseline data need to be collected over a long enough period to understand natural fluctuations and how they might relate to habitat factors such as drought. In this case, a baseline might reference the average density over a five-year period or the maximum number of flowering stems within any four-year period.

Once the parameters are identified and the baseline established, quantitative goals should be articulated as the third step. For an occurrence of *Carex polymorpha,* the goal might be a total population size of more than 5000 ramets with at least 25% setting seed and a canopy cover of 10–30%. Zaremba (1992) established a conservation goal for a population of the annual *Agalinis acuta* at a site in New York, of maintaining an average of 1000 plants over a five-year period at 8 to 10 subpopulations. These subpopulations should occur in good quality natural communities that are maintained by management that simulates natural processes.

The last step in setting conservation goals is to establish a "red flag," or lower threshold, for the parameters measured that will alert the manager to problems and the need to re-evaluate management strategies or to review conservation goals. This re-evaluation is an important step because the manager needs to know when to intercede in the management process in order to avoid extirpation of the population.

SITE MANAGEMENT PLANS

Site management plans drafted as part of the site design process should now be fleshed out. The purpose of the plan is to document our ecological and management assumptions and to spell out the management policies and actions that need to be implemented to accomplish the conservation goals. I am not proposing a rigid format for these plans. What is most important is that they be dynamic, capable of being reviewed and updated on a regular basis. A management plan should never be bound! It might be useful to think of a management plan as a file drawer where information can be added, replaced or updated easily. Information in this plan can be classified as archival and active. Archival information would include items such as species lists, resource maps (soils, vegetation, etc.), land use history, research results and legal documents, while the active portions of the plan would include the ecological model, goals, policies, management prescriptions, monitoring plans and results, lists of next actions or action plans, and budgets. Once again, the format of the plan is not critical; documenting our ecological and management assumptions and spelling out management policies and actions are.

BIOLOGICAL MONITORING

The last stage of the management planning process which I wish to address and emphasize because of its importance and role as a feedback mechanism is biological monitoring. Monitoring means many things to many people but virtually all monitoring activities share (or should share) three common traits. First, monitoring actions are repeated over time; second, monitoring results are interpreted by comparison to some standard or objective and finally, the results of monitoring are always subject to interpre-

tation. Biological monitoring indicates what is happening but does not answer any hypotheses; it does not tell you why. Taking one's temperature is a form of monitoring. The standard or goal a person is trying to achieve is 98.6° F; a high temperature indicates something is wrong, but not what.

For the past six years The Nature Conservancy has been using and promoting a very narrow definition of monitoring in the context of the management process discussed in this paper. The Conservancy defines biological monitoring as tracking or auditing of species and communities relative to stated conservation goals. Biological monitoring, then, has the explicit objective of describing a species' status at a point in time, and its trend in status over time. A monitoring program allows land managers to evaluate whether their management decisions, including the decision to leave the system alone and do nothing, are correct (whether conservation goals are being attained) and similarly whether the status and trend in status of the species indicate that it is time to review the ecological and management assumptions and either revise the management program or revise the conservation goals. This monitoring will not tell us why we did not reach our management goals. Similarly, this monitoring is not designed to set management prescriptions. The distinction is important. I consider the questions of causation and comparisons of management prescriptions to be research and to be addressed by a research program. A monitoring program is an ecological audit whose function is simply to identify where things are working and where they are not.

All *in situ* management programs should have a monitoring program to evaluate their success. Palmer (1986) conducted a review of monitoring programs in a number of states. The Nature Conservancy followed up with a review of their own programs. Based on results of these two surveys a number of recommendations can be made which will help ensure a successful biological monitoring program and wise use of limited conservation resources.

1. Set conservation goals and red flags. Conservation goals need to be developed for each monitoring program. Without measurable goals, biological monitoring will simply detect change, and change in any biological system is a given. Without a goal it is difficult to determine what changes are pos-

itive and what negative. Finally, without a goal it is difficult to decide what parameters need to be measured, resulting in monitoring programs that attempt to look at everything or look at the wrong parameters. "Red flags" warn the manager when it is time to reevaluate management assumptions and initiate new management actions, including research.

2. Keep methods simple and focused on goals. Methods need to be focused on selected parameters; if goals are clear and well formed, methods tend to fall into place. Ill-conceived goals result in weak methods which become subject to frequent change as goals are reinterpreted. Methods need to be as simple as possible to measure status of the key parameters. Methods capable of being carried out by volunteers are the best and increase our capacity.
3. Document methods. Each monitoring program should have a clear plan that describes the methods and goals. Long-term continuity of the program depends on development of a monitoring plan.
4. Plan for analysis of data. Too many monitoring programs do not address how the data will be analyzed. Methods of analysis need to be stated up front in the plan to ensure that data collection methods are adequate.
5. Get monitoring plans reviewed. It is always valuable to get outside review and opinions. Of course, without a monitoring plan there is nothing to review.
6. Provide for data storage. Storage of raw and processed data needs to be considered in a monitoring plan. Processed data should be stored and managed so that results can be easily accessed, communicated and summarized.

The Biological and Conservation Data system (BCD) used by the Natural Heritage Program Network in all New England states provides for the tracking of the status and trends of species and community occurrences through monitoring datafiles that can be linked to all species and communities in the Heritage Data Network. BCD, then, can be used to record every monitoring event (Ecomonitoring Visit Record) and to summarize these events (Ecomonitoring Record) to provide a picture of the overall status and trend in status of the species or community monitored. Formats are shown in Figure 3.

ECOMONITORING RECORD

1. Monitoring Subject: _____
2. Location: _____
3. Goals & Objectives
   Management Plans: Y/N Monitoring Plan: Y/N Monitoring Level: 1,2,3
   Management Goals: _____
   _____

Parameter	Goal	Red Flag
1. _____	_____	_____
2. _____	_____	_____
n. _____	_____	_____

4. Monitoring Procedures
   Methods: _____
   _____
   Sampling Frequency: _____
   Visit Dates: 1. _____ 2. _____ n. _____ } From Ecomonitoring Visits Record
5. Trends and Recommendations
   Short Term Trend: _____ Long Term Trend: _____
   Trend Interpretation: _____
   _____
   Current Condition: _____
   Condition Comments: _____
   _____
   Trend Update: _____
   Management Recommendations: _____
   _____
   Monitoring Recommendations: _____
   _____
   Location of Raw & Processed Data: _____
   Update: _____

ECOMONITORING VISITS RECORD*

Visit Code: _____
Visit Date: _____
Observer: _____ Person Hours: _____
Effort Comments: _____
_____

Parameter	Quantitative Summary	Qualitative Note
1. _____	_____	_____
_____	_____	_____
2. _____	_____	_____
_____	_____	_____
n. _____	_____	_____

Other Observations: _____
_____

* One record produced per monitoring event

Figure 3. Formats of Ecomonitoring and Ecomonitoring Visits records used in the Biological and Conservation Data System.

SUMMARY AND RECOMMENDATIONS

A balanced conservation program with a goal of protecting rare plants needs to address *in situ* as well as *ex situ* protection strategies. To succeed, an *in situ* program requires more than setting aside land for conservation purposes; many of the threats faced by plant populations and their habitats require a carefully planned program of habitat management that addresses both the appropriate uses of the site and the need for active biological management. Almost 50% of the most ecologically significant sites in New England occur, at least in part, on public land. Since use and management goals of many publicly owned sites do not reflect their ecological significance or specifically address conservation of rare species, my first recommendation is:

1. The New England conservation community should support and promote programs aimed at: a) alerting public land management agencies and land managers of the occurrence and significance of rare plant populations on their holdings, b) raising the level of protection on these lands, and c) providing habitat management information and assistance.

Protection and habitat management decisions for specific populations of rare species are best made after looking at the range and status of the entire species. Each occurrence needs to be evaluated on the basis of its contribution to protection of the species. This evaluation is critically important because of a need to focus limited conservation resources where they will have the greatest effect. My second recommendation is:

2. The New England conservation community should support and promote a range-wide approach to conservation planning for individual plant species by utilizing data and data structures found in and produced by Natural Heritage programs in each New England state.

Planning for the conservation of a species requires a coordinated and non-redundant effort on the part of many conservation players—members of the conservation and academic communities as well as private and public land managers. My third recommendation is:

3. Following existing models, the New England conservation community should promote use of protection planning

meetings to include, as needed, land managers, conservationists and scientists capable of significantly contributing to protection of a species and its habitat. These meetings should focus on and result in conservation action by identifying needs, assigning responsibility to specific individuals and agencies for next-step type actions and tracking progress toward accomplishing these actions.

When a decision is made to focus conservation resources on a particular plant population, a habitat management planning process needs to be implemented. This process begins with collection of all available information/data on the species, the population of interest, its habitat and the site in general. This information should be summarized into an ecological model or description of the life cycle of the species, dynamics of the species and its habitat, and biotic and abiotic factors affecting them. This model is used to identify land needing protection attention, to develop specific measurable conservation goals, to identify information gaps and research needs, and to guide specific habitat management activities.

4. The New England conservation and academic communities should focus resources on applied research that will contribute to our understanding of biotic and abiotic factors affecting endangered species and their habitats. This work should include studies to determine minimum viable populations and result in development or refinement of ecological models to advance *in situ* protection efforts.

Development of the above ecological model improves our ability to design sites which are defensible, require minimum management intervention and provide the best chance for long-term protection and viability of the population in the context of its habitat. Site designs should precede any land protection efforts.

5. For all populations of rare plants targeted for *in situ* conservation, whether on public or private land, the New England conservation community should promote development of detailed site designs driven by our understanding of system function, and threats to and processes acting on the population and its habitat. These designs should include maps of lands needing protection attention, land protection

strategies, preliminary habitat management plans and cost estimates.

Development of concrete measurable conservation goals that articulate what we are trying to accomplish at a site is necessary, for we can never determine whether our protection and management efforts are successful unless we can articulate what success is. Site management plans need to be written to document management policies and actions and the assumptions behind them.

The last step in the habitat management process is development of biological monitoring programs which will measure our success at meeting the stated conservation goals, and if necessary lead us to reevaluate our ecological and management assumptions as well as the conservation goals themselves. This process leads to my last four recommendations:

6. For each plant population targeted for *in situ* conservation (including reintroduction efforts), measurable conservation goals should be developed. These goals should be unambiguously stated and revolve around one or more parameters of the population and habitat that best indicate health. Negative, or "red flag" goals should also be developed which will warn the land manager that management is not working and ecological and management assumptions need to be reevaluated.
7. For each site, management plans need to be developed which document ecological assumptions (ecological models) that the manager is working with, and spell out management policies and management actions. While no format is proposed, these plans should be dynamic, changing as information becomes available.
8. Biological monitoring programs need to be developed at each site targeted for *in situ* protection. These monitoring programs must be documented to ensure long-term continuity and aimed at collecting the minimum amount of data needed to evaluate progress at meeting conservation goals.
9. All of the data driving and derived from the planning process (including the programs, needs, procedures and results of biological monitoring, management and research, species and community dynamics, and results of site designs) should be stored and managed within the Network of Natural Heritage Programs and their cooperators (e.g., USFWS, USFS,

TNC). These programs have the data structures in place to manage this information and facilitate data exchange and communication.

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THE NATURE CONSERVANCY
EASTERN REGIONAL OFFICE
201 DEVONSHIRE ST., 5TH FLOOR
BOSTON, MA 02110-1402

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SCIENTIFIC AND POLICY CONSIDERATIONS IN RESTORATION AND REINTRODUCTION OF ENDANGERED SPECIES

DONALD A. FALK AND PEGGY OLWELL

"*Restoration, hang thy medicine on my lips.*"
—*King Lear,* Act IV, Scene 3

Like Cordelia's impassioned prayer in the closing moments of Shakespeare's greatest tragedy, the world of conservation is turning increasingly to the healing powers of ecological restoration for salvation. At least three national organizations—Society for Ecological Restoration, Natural Areas Association, and Restoring the Earth—are devoted to promoting intensive habitat management and ecological restoration as strategies for conserving biological diversity. Federal land-managing agencies as well as the largest private land conservation organizations, notably The Nature Conservancy, are engaged increasingly in various forms of reintroduction and restoration practice. Many members of the national Center for Plant Conservation network are playing an active role in replacing extremely rare and threatened species back into natural areas. Even the mainstream media have taken notice (Nash, 1991), as have many corporations whose activities have a major impact on the land and the life it supports.

But is reintroduction always a feasible or appropriate tool with which to perpetuate biological diversity, ecological processes and the grand dance of evolution? Experience reveals that reintroduction efforts frequently encounter substantial technical obstacles and may entail such a high degree of uncertainty that their value as a tool for conservation can be questionable. The biological value of reintroduction remains largely a matter of informed speculation, although the evidence supports cautious optimism. And the strategic and political implications of an improved ability to translocate plants are just beginning to be understood, including the chilling possibility that reintroduction will, through its application in mitigation programs, rationalize and even facilitate the destruction of existing natural areas.

In the face of such uncertainty and peril, why are conservationists thinking at all about moving or transplanting rare species?

At least three environmental conditions compel consideration of this activity:

1. Continued Destruction of Habitat

Despite decades of heroic effort, the continent's remaining undisturbed natural areas continue to be strip mined, logged, paved and fragmented. The Nature Conservancy—the most successful and most important private land conservation organization in the history of the country—has managed to protect on the order of 5 million acres, amounting to approximately .22% of the land area of the United States. Many states with the highest indices of plant diversity, including Hawaii, California, Texas, Florida and Puerto Rico, have major areas of habitat (encompassing whole endemic community types) on land that is unprotected and under active commercial development. In the state of Hawaii alone, as many as 95 *new* golf courses are proposed and awaiting construction permits to consume some of the last remaining level lowland habitat in the islands (Hawaii Office of State Planning, 1991). Wallace (1990) describes an analogously critical context for the sand scrub communities of central peninsular Florida. Pressure is increasing in many states to open public lands for large-scale strip mining for minerals; substantial lands are owned privately by mining corporations with plans for operations covering hundreds of thousands of acres. Equally intense pressure exists in tropical regions (e.g., Holden, 1986).

In the face of such destruction, rare plants are inevitably the first to suffer. Of the approximately 20,000 plant taxa native to the United States, 4412 (22%) are in the top endangerment categories in the ranking systems of the U.S. Fish and Wildlife Service, The Nature Conservancy, or the Center for Plant Conservation (Center for Plant Conservation 1992). Of these plants, 2768 (about two thirds) are restricted to a single state or province. Hawaii has 547 endemic rare taxa. The California Floristic Province includes 4450 taxa of plants, of which 2140 (48%) are endemic to the region (Myers, 1990). On a continental basis, 1183 (39% of the total flora) are known from five or fewer populations or from 1000 or fewer individuals. Not surprisingly, these taxa have the least margin of survival in the face of habitat loss and the greatest vulnerability to extirpation of populations and the loss of evolutionary viability. Even where entire species have not

been driven to extinction, many species are becoming severely depleted due to loss of genetically distinct populations. As Ehrlich (1991) observes, "extirpation of populations is the dominant element of the extinction crisis in temperate regions today and most severely threatens ecosystem services in these areas."

2. Habitat Degradation

Even where land is formally protected from outright destruction, significant deterioration of habitat can occur and with it the loss of the ability of many plants to adapt and survive. For instance, well over two-thirds of the total land area of the United States west of the Rocky Mountains is owned and managed by various agencies of the Federal government—Bureau of Land Management, U.S. Forest Service, National Park Service, Department of Defense—as well as the significant acreage reserved for Native American Indians, primarily in the southwest. Many of these lands are severely overgrazed, eroded, logged and overrun with recreation vehicles. Biological invasion by exotic organisms can so thoroughly alter habitat characteristics that the composition of entire communities is altered (Vitousek et al., 1987; Brockie et al., 1988; Vermeij, 1991). Millions of acres of Great Basin and northern Great Plains grasslands, for example, have been invaded and altered by exotic grasses such as red brome (*Bromus tectorum*) and other exotic species, reducing the native perennial bunchgrass communities.

Many rare plants are endemic to specific community types, or restricted primarily to specific seral stages. Fiedler (1986; Fiedler and Ahouse, 1992) and others (Kruckeberg and Rabinowitz, 1985) have described a variety of patterns of rarity, including such ecological and evolutionary factors as the relationship of edaphic endemism and restricted ecological amplitude to geographic rarity. Habitat endemics, a category that includes a large proportion of rare American plants, are often sensitive to alteration of physical or biotic characteristics of site and hence vulnerable to decline even if the site has not been completely or visibly "destroyed."

3. Large-Scale Climate Change

As Peters (1988) has described, current trends of climate change may render many protected areas unsuitable to maintain the spe-

cies that presently occur within their boundaries. Correspondingly, as the appropriate climatic zones for species migrate toward the poles, the optimal range for many plants will shift into areas of land that are currently unprotected. Much of this change is projected to occur at a rate tens or hundreds of times faster than plant populations can "migrate" generationally across the landscape (Schwartz, 1992).

These effects will likely be most severe for species that are restricted in their geographic distribution and ecological range. For example, species found in coastal areas, wetlands, montane-alpine and arctic biomes, and microclimatic refugia (such as the Appalachicola River Basin of Florida and southern Georgia) stand to experience drastic reduction or movement of their preferred habitat. The same would be true for the Hawaiian flora, which is more than 95% endemic to the Islands; many taxa are found on only a single island, at specific elevations and aspects to prevailing wind directions. Species occurring in few sites or in small populations will be the most vulnerable, a category that (as noted above) includes as many as two-thirds of all sensitive species in the United States. If these species are to survive at all, serious and active intervention into their management, including intentional alteration of their geographic distribution, will be essential. Combined with the effects of habitat destruction and degradation, many of these plants will not survive without such measures.

These three factors, among others, suggest that reintroduction and restoration will play a vital role in conservation strategies in the coming decades (Falk, 1990b; Edwards, 1990; IUCN, 1992; McMahan, 1990). Limited experience suggests that these methods may provide an enormously positive supplement to land protection, especially in helping to preserve individual populations. Such developments, however, do not take place in a political vacuum. Many of the societal forces contributing to the destruction of natural areas are seizing on the ability to translocate organisms as a way to rationalize or facilitate further destruction of habitat, rather than as a tool to repair damage that has already been done. Continuing threats to the Endangered Species Act, and to the basic legislative provisions for the protection of land in its natural state, will make such misuses of reintroduction even more dangerous. Certain regions of the country, notably southern California, peninsular Florida, and coastal Hawaii, are already

experiencing such overwhelming population growth and development pressure that the few regulatory restrictions protecting land seem like a fragile dam about to burst. When this happens, whether in a continuing trickle of incremental loss of habitat or a catastrophic deluge, the ability to reintroduce species will play a pivotal role in the survival of many species. The question will then become: when all of the suitable land has been destroyed, where can they be introduced?

REINTRODUCTION AND THE U.S. ENDANGERED SPECIES ACT

The Endangered Species Act of 1973, as amended, provides the legislative authority for the use of reintroduction as a conservation tool in the recovery process for federally listed endangered and threatened species (U.S. Fish and Wildlife Service, 1988). However, reintroduction has been controversial from both the economic and scientific perspectives. It was the economic conflicts and concerns that prompted Congress in 1982 to amend the Act to include a special provision for experimental (reintroduced) populations (Drabelle, 1985).

Within Section 10(j) of the Act (U.S. Fish and Wildlife Service, 1988), experimental populations are allowed to further the conservation of the species. An experimental population may be classified as either "essential to the continued existence of the species" or "nonessential." If the reintroduced population is deemed "essential," then the population is treated (for purposes of the Act) as though it is a threatened species. Thus, the population is awarded all the protection of a threatened species under the Act. However, if it is deemed "nonessential," then it is treated as though it is a proposed species under the Act, thereby receiving less protection than the essential population. These designations allow the U.S. Fish and Wildlife Service more options in managing the reintroduced populations.

Since 1982 when these amendments were developed, only seven experimental populations have been listed under the Act; all have been for vertebrate animals (J. Sheppard, pers. comm.). However, plant reintroductions are occurring regularly without formal listing as experimental populations under the Act. Instead, they are being conducted without the legal designation of the Act through multi-agency and/or private cooperative efforts.

Table 1. Recovery plan status of 239 federally listed plants, as of 1990.*

Plan status	No.	(%)
Approved	119	(50)
Draft	71	(30)
None	49	(20)
Total	239	(100)

* Source: U.S. Fish and Wildlife Service (1990a).

In a review of plant recovery plans for their report to World Widlife Fund, Cook and Dixon (1989) found that the predominant threat to rare plants, not surprisingly, is habitat disturbance or destruction. Sixty-six percent of the species they reviewed were threatened by loss of habitat. Thus, site preservation should be the first priority in a recovery plan. However, the authors also indicated that the second priority in developing a recovery program for rare plants should be "the identification of potential habitat and the development of techniques to establish new populations." Obviously, Cook and Dixon view the reintroduction of endangered plants as a viable means of enhancing the conservation of these species.

There are others who believe reintroduction can be beneficial to the recovery of endangered plant species (*see* Jones, 1990). For example, the U.S. Fish and Wildlife Service's 1990 report to Congress revealed that for the 239 listed plants, only 50% (119) had approved recovery plans and 30% (71) had draft recovery plans (Table 1). However, reintroduction was either in progress or planned as part of the recovery efforts for 56 listed plants (Table 2). Additionally, of those 56 species, 42 had reintroduction as one recovery criterion for downlisting or delisting the species. Therefore, almost 25 percent of the federally listed plants, as of 1990, have reintroduction as a tool for the recovery of the species (U.S. Fish and Wildlife Service, 1990a). This number of species with reintroduction as a major focus or effort for recovery is surprisingly large, especially considering that the U.S. Fish and Wildlife Service does not have a specific policy on rare plant reintroductions or guidelines on how to conduct rare plant reintroductions (U.S. Fish and Wildlife Service, 1990b). Essentially, the Service's only policy guideline on reintroductions is that they should not occur outside the historic range of the species unless approved by the Director (U.S. Fish and Wildlife Service, 1990b).

Table 2. Federally listed plant taxa with reintroduction projects, as of September, 1990.*

Taxon	Current[1]	Planned[2]	Down/ De-listing Criteria[3]
Amorpha crenulata			X
Amsinckia grandiflora	X	X	X
Amsonia kearneyana	X		
Arctostaphylos pungens ssp. *ravenii*	X		X
Asimina tetramera	X	X	X
Astragalus phoenix			X
Astragalus robbinsii var. *jesupi*			X
Banara vanderbiltii			X
Betula uber	X		X
Boltonia decurrens	X	X	X
Buxus vahlii			X
Calyptronoma rivalis	X	X	
Centaurium namophilum			X
Cornutia obovata			X
Crescentia portoricensis			X
Cyathea dryopteroides			X
Daphnopsis hellerana			X
Dicerandra immaculata	X		X
Enceliopsis nudicaulis var. *corrugata*			X
Geum radiatum	X	X	
Goetzea elegans			X
Grindelia fraxinopratensis			X
Harperocallis flava	X	X	X
Hibiscadelphus distans		X	
Hymenoxys acaulis var. *glabra*	X		X
Hymenoxys texana			X
Ilex cookii			X
Iliamna corei		X	X
Isotria medeoloides			X
Ivesia eremica			X
Kokia cookei	X	X	
Lesquerella filiformis	X		
Liatris helleri			X
Mahonia sonnei			X
Mentzelia leucophylla			X
Nitrophila mohavensis			X
Oxypolis canbyi			X
Panicum carteri		X	
Pedicularis furbishiae			X
Pediocactus knowltonii	X	X	X
Pediocactus pebblesianus var. *pebblesianus*			X
Peperomia wheeleri			X

Table 2. Continued.

Taxon	Current[1]	Planned[2]	Down/ De-listing Criteria[3]
Phacelia argillacea		X	X
Potentilla robbinsiana	X	X	X
Ranunculus acriformis var. *aestivalis*		X	
Rhus michauxii	X	X	
Sarracenia oreophila	X	X	
Sidalcea pedata			X
Solidago spithamaea			X
Stephanomeria malheurensis			X
Styrax texana	X		
Thelypodium stenopetalum			X
Torreya taxifolia			X
Trichilia triacantha			X
Trifolium stoloniferum		X	
Zanthoxylum thomasianum			X
TOTALS	18	17	44

* Source: U.S. Fish and Wildlife Service (1990a).

[1] Any reintroduction project occurring in the past few years (1986–1990) or since any previous reports.

[2] Any reintroduction project to be continued or initiated during 1991 and 1992.

[3] Any reintroduction project that is included in the criteria of an approved or draft recovery plan.

SCIENTIFIC POLICY CONSIDERATIONS IN SPECIES REINTRODUCTIONS AND ECOLOGICAL RESTORATION

The term "policy" carries as many uses as there are users, but in one form or another generally involves asking, "What should we do? How do we propose to act? What are our goals? (Faludi, 1973). In the present instance, identifying a clear long-term *objective* for plant reintroductions is of central importance—an exercise of considerable difficulty. For example, do we intend to maintain *all* species in their current abundance and distribution, or to reduce some and augment others? Do we wish to return all native species to their pre-Columbian distribution and eliminate all exotic invaders? Is the distribution of species intended to remain static or to change over time (and if so, in what way)? Is it our intention, as population biologist John Harper once asked a conservation meeting, "to make rare plants common"? Do we propose to manage habitat actively, or to allow ecological and

Table 3. Nomenclature employed in published literature describing activities involving movement of living organisms to and from habitat, shown with the generally associated level of biological organization.

Term	Level of Biological Organization
Relocation, translocation, transplantation	Individuals, populations
Augmentation, enhancement	Populations
Introduction, reintroduction	Populations, species
Revegetation	Communities
Restoration, rehabilitation, reconstruction	Communities, ecosystems

evolutionary processes to operate without interference (other than the colossal disruption we are already causing by environmental degradation)?

As these questions are meant to illustrate, a true societal consensus on any of these points is highly unlikely. In fact, even within (and between) the conservation and scientific communities there is considerable disagreement on almost every point. Some conservation biologists oppose any moving of organisms, as a disruption of the natural distribution of genetic (and hence evolutionary) variation. Others endorse replacing species in historically documented localities, but only where populations have been recorded previously. Still others encourage placement of threatened species on any suitable protected land, as a pragmatic crisis strategy to prevent further anthropogenic extinction (*see* IUCN, 1987).

"Policy" is not made in the abstract; it represents the collective decisions and intentions of any organized group in society, whether a botanical club, conservation group, mining corporation, trade lobbying organization, or the Federal government. Furthermore, policy is meant to organize behavior in such a way as to promote fulfillment of that group's objectives and mission. But since the objectives and interests of various groups affecting nature may be fundamentally different (and even mutually exclusive), the priority accorded to different goals—such as protecting biological diversity as compared to returning a profit to stockholders—will vary dramatically and predictably. Moreover, one cannot presume to make policy for another group; one can only articulate one's own, and to describe the considerations one believes should be taken into account.

Consideration of these questions for biodiversity management

is further complicated by inconsistent and rapidly changing terminology. The literature includes references to introduction, reintroduction, relocation, translocation, transplantation, revegetation, restoration, rehabilitation, augmentation, enhancement, and other terms. Many of these carry specific meanings, while others are used variously or interchangeably. Although the untangling of this nomenclature is beyond the scope of this paper, it is useful to note that each term generally refers to a particular level or range of biological organization (Table 3). For purposes of this paper we will employ the terms "reintroduction" and "restoration" to refer to the relevant actions for populations of rare plants and their associated communities and ecosystems.

Good policy is ultimately dependent upon asking good questions, which are the *sine qua non* of clarity. For that reason, we attempt here to outline some of the basic questions that should be asked, or considerations taken into account, in preparing a reintroduction program. The *questions* are categorical; the *answers* will be case-specific. That is the work of planning a good reintroduction effort.

As a contribution to this process, the Center for Plant Conservation is presently undertaking a national study of reintroduction and mitigation policy with respect to rare plants. This will include a comparative review of the policies of major Federal and State land-managing agencies and private land-owning organizations, and the formulation of proposed guidelines.

In assessing reintroduction as a strategy for conserving rare plants, a series of five areas of inquiry emerge. First, we should always be clear *why* we are undertaking a reintroduction program, and consider carefully what our long-term goal is with respect to the proposed project. Next, we need to consider the *consequences* of a reintroduction effort, including the possible implications for the protection status of existing populations and habitat. Third, we must assess *where* the reintroduction takes place and *who* will be involved in maintaining and managing the population. These considerations have a major bearing on the probable long-term viability and success of the reintroduction effort. Fourth, we need to understand *how* reintroductions should be conceived and carried out from a biological perspective, and the prospect that these actions will contribute to the achievement of a long-term conservation goal. And finally, we must ask *if* reintroduction in a

particular case is even technically possible; if not, the option is eliminated from consideration until further research opens the possibility. These five general areas of consideration may be described respectively as (i) objective, (ii) strategic, (iii) managerial, (iv) biological, and (v) technical.

We propose these factors not only as a conceptual framework for thinking about reintroduction and restoration issues, but also as a *decision-making sequence* for well-conceived practical programs. Although we discuss them as separate considerations, we acknowledge that they are highly interactive, and frequently difficult to separate. For example, the absence of a pollinator or seed dispersal agent may raise questions both about the technical feasibility of a reintroduction project, and about its long-term biological significance. Likewise, the strategic consequences of a reintroduction project for the protection of other natural populations may be deeply influenced by administrative factors such as land ownership and the commitment of the land-managing agency to proper ongoing management. Nonetheless, we maintain that reintroductions should above all be well-conceived and well-planned in order to be successful, cost-effective, and contributory to the overall objectives of conservation, and that approaching the planning process in the order described will contribute to prospects for success.

In our experience, many reintroduction efforts begin with careful study of technical feasibility and biological considerations, and only later (or incidentally, or not at all) address the strategic and political consequences of the action. We suggest that this is a significant error, both tactically and procedurally, for several reasons. First, reintroductions should always be undertaken in relation to a clearly stated long-term objective; otherwise, they are simply stochastic events with little prospect for cumulative effect. Second, careful planning can ensure that the project will be carried out efficiently and cost-effectively. Managerial and strategic considerations have a particularly large bearing on prospects for success, both for the immediate reintroduction itself and for protection of other similar populations or communities. And lastly, technical and biological obstacles are the most amenable to resolution by research, experimentation, or simple trial and error; in fact, their resolution may be built into the implementation sequence for the project itself.

1. Objectives

Although it frequently runs counter to our established habitual ways of acting, we submit that thinking about reintroduction programs should start with clarity regarding objectives and strategic implications. Once these overall contextual decisions are made—is reintroduction a good idea? does it meet our long-term objectives?—the more immediate technical and biological concerns may be addressed and incorporated into the project design.

As Millar and Libby (1989) observe, reintroduction and restoration projects can recreate viable, complex, sustainable communities—or "Disneyland" simulations. The determination of long-term objectives is a non-trivial undertaking for anyone working to protect biodiversity in the face of continued development pressure and economic constraints. The days when conservationists could realistically envision large areas of the continent in a wild and natural state are gone, perhaps forever. Instead, we must reorient our efforts to a different set of goals involving the integration of human activities into a matrix of natural biological diversity and functions. As Diamond (1987) notes, even such watchwords as "natural" and "self-sustaining" need to be examined critically and realistically. For many areas of the continent the objective may become to re-establish diversity in a perpetually managed setting—a far cry from self-sustaining, undisturbed systems (Diamond, 1985).

Goal-related issues concerning a reintroduction program might include the following:

1. Are there clearly articulated long-term goals for conservation of the species or community type? What are these goals?
2. Is the goal to re-establish "pre-disturbance" distribution and abundance? If so, what point in the species' or community's natural history do we propose to re-establish? Are distribution and abundance stable, trending, or undergoing long-term oscillation (Falk, 1990a)?
3. What forces influenced the distribution and abundance of the species or community prior to the "disturbance"?
4. Is elimination or amelioration of the cause of decline or threat to species part of the project?
5. Once reintroduction or restoration has taken place, what will happen? Is there a commitment to provide intensive

management indefinitely, or eventually to allow natural successional and ecological forces to prevail?

6. Do we propose to maintain every species and community in perpetuity, or to allow some to change or disappear over time? If the latter, what criteria will we use to make these decisions?

As is evident, some of these questions border on what many practitioners would consider philosophical issues beyond the realm of conservation, or at least beyond their mandate and responsibility. Nothing could be further from the truth; unless these basic issues are addressed and at least partly answered, the efforts of individual agencies with particular sites, species, or communities will have no organized relationship to a long-term goal. Answers may be elusive and difficult to pin down, and the criteria seemingly impossible to establish, but a reintroduction plan will be greatly strengthened by inclusion of these factors in its reasoning, to the extent that they can be addressed.

2. Strategic Considerations

By their very nature, most reintroductions take place in the context of conflicts over land use, enhancing or re-establishing populations destroyed by incompatible uses. Usually at issue is the priority accorded protection of biological diversity versus resource extraction, recreation activities, or other extensive modifications of the landscape. While some of these decisions are made internally by a single agency thinking about its own land, such as the multiple-use paradigm of the Bureau of Land Management or the U.S. Forest Service, most involve conflicting mandates and interests of more than one organization, often in an adversarial relationship.

The most serious contextual consideration for the current practice of reintroduction in the United States is the practice of *mitigation.* Mitigation almost always involves a trade of some kind: land for land, land for money, land for long-term management support. Typically, a developer will propose to establish "new" habitat equivalent to that being destroyed by the project. Variables may include the amount of land involved, financial support, long-term ownership and management responsibility for the created habitat, quality and success assurances, and the relationship

to large-scale bioregional strategies for maintaining ecological diversity.

Formally speaking, to "mitigate" means to reduce or ameliorate the impact of an action, to lessen its severity and alleviate or abate its consequences. Many "mitigation" projects are anything but; instead of reducing the impacts of development pressure, in reality they have become a means of justifying *increased* invasion of protected areas. In certain parts of the United States, regulatory agencies now receive hundreds of requests for mitigation projects involving the destruction or substantial modification of natural habitat, in exchange for the creation of "new" habitat elsewhere. On a regional basis, mitigation appears to be most heavily practiced in southern California, peninsular Florida, and parts of the southwest and southeast. Specific habitats, however—notably, wetlands and riparian areas—are being heavily affected in all parts of the country. Wetlands habitats are naturally among the most controversial subjects for mitigation proposals. Given their complex energetic and nutrient webs, species composition, and hydrology, wetlands represent extraordinary challenges for habitat creation or even individual reintroductions (Jarman et al., 1991; Munro, 1991). Yet Dobberteen (1989) found over 1000 wetlands creation projects in Massachusetts alone in just seven years beginning in 1983!

A frequent problem with many mitigation projects is that they are undertaken in the absence of a consensus on long-term goals. For instance, there is considerable evidence that re-created habitats may take decades to become fully established; until this has occurred, there is little assurance that the reintroduced population or created habitat will serve the same ecological and evolutionary functions as those that were destroyed. Long-term issues of land protection may remain unresolved, leaving the reintroduced population or created site vulnerable to future disruption or even destruction. This is especially true for lands under private or corporate ownership.

Most critical, however, is the relationship of mitigation programs to the conservation of existing natural areas. Again, this is fundamentally a matter of agreeing upon objectives. For a developer, the objective may be to build a desired project, and to provide mitigation tradeoffs only to the extent required by law, regulation, political expediency, or a desire to maintain a good public image. Conservationists, on the other hand, may approach

mitigation primarily as a strategy to assist the protection of ecologically valuable or unique communities, species, and populations. The regulatory agency involved may operate strictly by the letter of the law, with no particular vision for the future. The overlap between these three different agendas can prove to be narrow ground indeed on which to build a sound future for habitats or threatened species.

By and large, standards for the practice of mitigation projects involving endangered species do not presently exist at the national level. Individual agencies have been developing policies incrementally, but even the largest Federal agencies manifest considerable internal variability in how they approach mitigation proposals. In the meantime, individual states, counties and private corporations all develop, evaluate and implement mitigation proposals in increasing numbers, without the benefit of either a true consensus on goals, or clear national guidelines.

A reasonable starting point for such standards would be that *mitigation projects should never entail the destruction of existing significant and irreplaceable natural areas. Reintroduction and restoration should, in other words, be employed to heal damage that has already been caused, not to rationalize further destruction.* This is analogous to the Hippocratic oath taken by physicians to "do no harm" in using their skills and knowledge (E. Guerrant, pers. comm.). In part, this position reflects a realistic assessment of the uncertainties of ecological restoration; the probability is extremely high that a created habitat or reintroduced population will be different in some essential aspects from the one it replaced, if it succeeds at all. More profoundly, it acknowledges that we still understand very little about the life history, interactions and evolution of most organisms in their natural state, so that a degree of humility is in order before we proclaim "success."

The strategic relationship between existing diversity and proposed reintroductions is especially important for habitats or populations that may be difficult to replicate; in this respect there is a strong linkage between the degree of knowledge about the biology of a species or community proposed for reintroduction, and the strategic implications in undertaking such a project. For example, "no net loss" wetlands policies assume that the technology and scientific understanding reliably exist to create replacement wetlands, when in fact no such knowledge base exists. As Zedler and Langis (1991) observe, decades may be required to ascertain

the successful establishment of coastal wetland communities; even then, full functional parity with undisturbed reference wetlands may never occur, due to basic differences in soil or hydrology. For example, their study of natural and constructed wetlands in San Diego Bay found that after five years the constructed wetland areas provided only slightly more than half of the ecological functional equivalency of the natural site, in terms of soil characteristics, nutrient availability, biomass, and species diversity. Furthermore, they saw little evidence that this performance would improve over time.

The same holds true for reintroduction projects with individual rare species. Reintroduction can play a useful role in helping to enhance damaged populations of rare species, to restore extirpated populations, or to establish new ones (Falk, 1990c; Falk and McMahan, 1988; Olwell et al., 1987, 1990). However, it can also be used intentionally by organizations with different objectives to justify the destruction of natural populations. In Western Australia, for instance, the successful results of a state-funded research project into propagation techniques for one of Australia's rarest terrestrial orchids at the Kings Park and Botanical Garden were used in part to rationalize the destruction of one of the few remaining wild populations (Dixon, pers. comm.).

In terms of establishing precedent for the future, mitigation represents a slippery slope. If carried to its logical extreme, any existing natural area could theoretically be subjected to a mitigation tradeoff. Success in restoration and reintroduction work is thus a mixed blessing: while we may celebrate the successful establishment of a new community or population, our very success may be used as a weapon against existing natural areas which we (but not others) are committed to protecting.

Strategic issues that should be raised in evaluating a restoration or reintroduction project thus may include:

1. Is the project consistent with large-scale regional strategies for protecting land and biological diversity (Jenkins, 1989)? Will the project establish a precedent that might indirectly weaken protection for other natural areas?
2. Will the project *directly* involve the destruction of any existing natural area? If so, what is the comparative quality of the proposed sacrifice and replacement areas? What are the chances that unique biological or landscape values will be

lost if the project proceeds? Are there any alternatives to this course of action?

3. What criteria were used in selecting the sacrifice area? Are they biologically sound and contribute to overall conservation objectives as identified in Step 1, Objectives, above?
4. Can impacts be directed to areas already disturbed and away from previously undisturbed sites?
5. How much acreage is involved in destruction and creation? Have sufficient areas been included for buffer zones, large-scale ecological processes, and movement of communities over time?
6. Has the project been costed-out over a realistic long-term financial schedule (King, 1991)? Is there a substantial net gain in funds available for conservation projects? How will unexpected future costs be borne, and by whom? Have performance bonds been posted that correspond to the time required to assess biological success?
7. Are there binding commitments by the land-managing agencies for permanent protection of the created habitat or reintroduced populations? What provisions have been made for monitoring and management (see Step 3, below).

3. Land Management and Administration

Introductions will most likely be of permanent conservation value if they are undertaken on land that is securely protected and managed for biological values. Long-term management in some form is essential for the maintenance of natural diversity on most protected areas in the continental United States, including even our largest natural areas and parks (e.g., Clark and Harvey, 1988). The "managed natural area" is no longer considered an oxymoron, but rather the dominant mode of preserving land and ecological values.

Management considerations are especially important for reintroduced populations of rare plants. Many species inhabit successional communities, or habitat parcels so severely fragmented that only intensive management can maintain their integrity. Reintroduction experience with *Pediocactus knowltonii, Penstemon barrettiae, Dicerandra immaculata, Stephanomeria malheurensis, Arctostaphylos uva-ursi* var. *leobreweri, Amsonia kearneyana, Styrax texana, Amsinckia grandiflora* and other species confirms

the importance of having a long-term management plan for a reintroduction site.

The case of *Stephanomeria malheurensis* (malheur wire-lettuce) provides a good case in point. The plant, which is of considerable scientific interest because of evidence that it is recently speciated (Gottlieb, 1973, 1991), is known only from its type locality in south-central Oregon. The population was virtually destroyed in the 1980's by grazing, fire and invasion by exotic species. Using seed collected at the time of the species' original description, the Berry Botanic Garden collaborated with the U.S. Fish and Wildlife Service, Bureau of Land Management, Center for Plant Conservation and others to re-establish the plant on the original site. Transplants were undertaken using four experimental ground covers, with the area fenced by the BLM. For the foreseeable future, the species will have a chance only if management measures are maintained; otherwise, the same forces that brought about its demise once would almost certainly do so again (Parenti and Guerrant, 1990). Such cases are more likely to be the rule than the exception with rare species reintroductions.

Several private companies have introduced or reintroduced rare species onto their lands following major disturbances from mining or construction operations. Such work is frequently mandated by state or Federal law and generally carried out as part of a master plan for post-mining land reclamation (Gillis, 1991). However, there is frequently a reluctance to establish, in the words of the environmental officer for one such firm, "species that carry a regulatory burden"—in other words, restrict the company's options for future land use. Given the weakness of the Endangered Species Act in its present form to protect plant species on private land, reintroduced populations on non-conservation land should probably be regarded as ephemeral unless the company is willing to sign a long-term conservation contract with a public agency or conservation group.

On the other hand, reintroduction can play a significant role in the recovery of endangered or threatened species, if integrated into long-term planning. An example is *Trifolium stoloniferum* (running buffalo-clover), for which a strategic recovery plan has been developed by the U.S. Fish and Wildlife Service, integrating legal status, site protection, establishment of reintroduced or enhanced populations and research (U.S. Fish and Wildlife Service, 1989).

Administrative and management considerations in planning reintroductions may include the following:

1. Does a recovery plan exist? If so, did the agencies responsible for implementation play a part in its formulation, and have they made a commitment to carry it out?
2. Is the reintroduction site under secure long-term protection?
3. Has the original threat(s) to the species or community been eliminated, or are there plans to manage the threat(s)?
4. What is the commitment of the land-managing agency to conservation and biological management? Is such activity basic or incidental to its primary interest?
5. Will there be on-going monitoring and management of the site? Will such activities maintain habitat for the species in question?

4. Biological Issues

Despite elevated public interest and attention in rare species, the base of knowledge about rare plants remains small. The first comprehensive volume on the subject (Falk and Holsinger, 1991) includes discussion of the genetics, population biology, demography and ecology of rare plants to the extent they are known, but in general one is struck by how little published data exist for most rare species. Symposia organized by the California Native Plant Society (Elias, 1987), Natural Areas Association (Mitchell et al., 1990), and Society for Ecological Restoration (Bowles and Whelan, 1992) have contributed a great deal of new information, as have research reports in the conservation biology literature. Specific aspects of the biology of rare plants in some genera—*Amsinckia, Astragalus, Calochortus, Cercocarpus, Clarkia, Helianthus, Pediocactus, Pedicularis, Platanthera* and *Stephanomeria,* for example—have been studied closely by one or more researchers, and there are now several hundred published citations of specific rare plant studies. But with over 4400 rare species in the United States alone, distributed in nearly 1000 genera, this is a thin knowledge base from which to successfully manage this diversity of species.

Much information about rare species remains anecdotal and unrecorded except for the internal documents and contracted reports of managing agencies. Recovery plans of the U.S. Fish and

Wildlife Service help to draw together references for individual species, but here again fewer than 6% of species of national conservation concern have been listed under the Endangered Species Act, and only half of those as noted above, have recovery plans. The detailed empirical observations of sanctuary and preserve managers, agency field staff, conservation horticulturists and amateur botanists are all of great value, but all too often these insights go unrecorded, and hence remain unavailable to all but a few people. Intensive research studies (such as Bowles, 1983) are extremely useful for reintroduction work; however, few rare plant species have ecological studies in sufficient detail.

Clearly, it will often be impractical to assemble a complete biological profile of every species or community before we begin engaging in conservation work. Consequently rare plant reintroductions will involve a substantial element of trial and error experimentation (Harper, 1987; Griffith et al., 1989). Unlike well-studied crops or range grasses, field reintroductions of rare plants involve species whose developmental, reproductive and ecological characteristics are little known. Information critical to understanding how to design an appropriate reintroduction, including the original biogeographic distribution, pollinators and seed dispersal agents, genetic architecture and long-term patterns of population growth, may be unknown. Present patterns of distribution may be so severely disrupted by anthropogenic causes that even the plants' preferred soil type may not be reliably determined. For example, the tallgrass prairie flora of the Great Plains now remains in such a small fraction of its original extent, and in such fragmented parcels of habitat, that it is difficult to know even which species were naturally rare and which were reduced to rarity by habitat modification. In Illinois, less than seven hundredths of one percent of the original prairie remains intact (White, 1978). Some entire communities, such as the tallgrass savannas, were virtually invisible because they had become so overgrown and invaded (Packard, 1991).

A classic New England example of the need for deeper biological understanding is the attempted translocation of *Isotria medeoloides* (small whorled pogonia) from a naturally occurring (but unprotected) site on the west side of Lake Winnipesaukee, New Hampshire, to nearby protected state land (Wilson, 1987). Originally undertaken to salvage plants from a condominium development on private land beginning in 1985, the reintroduced plants

have been monitored for recruitment, mortality and other parameters. The species is known to undergo long-phase oscillations in reproductive population (Mehrhoff, 1989), further complicating assessment of the size or status of the population at any given time; it is frequently difficult to distinguish such long-phase oscillations from linear trends for decline or increase in population size (Brumback, pers. comm.). Thus, a proposal to confidently relocate this species as part of a mitigation project would have to be met with considerable skepticism, patience, or both.

Most rare plant reintroductions involve outplanting of a subset of the genetic variation found within the species. As such, these efforts constitute empirical tests of several important hypotheses in population biology related to the genetic and evolutionary consequences of small population size: founder events and genetic bottlenecks, the effects of close inbreeding and the vulnerability of small populations to various types of stochasticity (Barrett and Kohn, 1991; Menges, 1991; Lewin, 1989). Although a few rare plant reintroductions (such as *Amsinckia grandiflora* by Pavlik, *Stephanomeria malheurensis* using material provided by Gottlieb, and *Hymenoxys acaulis* by De Mauro) have been carried out with baseline genetic data on the reintroduced individuals. until recently few have included such data or any provision to monitor changes in the genetic structure of the population over time. The result is two-fold: (i) collective knowledge of rare plants is not expanding as rapidly as it might; and (ii) many reintroductions will fail biologically for reasons that will not be fully understood.

In general, the rare plant literature supports the view that genetic variation found among populations is significant reproductively, ecologically and evolutionarily, and should be maintained in conservation work (Holsinger and Gottlieb, 1991; Templeton, 1991; Hamrick et al., 1991). Small differences among populations may represent incipient ecotypic differentiation or even the beginning of the speciation process. Moreover, a significant fraction of the total diversity in plants is found among populations (Hamrick et al., 1991). Approximately half of the allozyme loci in plants, on the average, are polymorphic (although endemic species are somewhat lower, with approximately 40% of their loci polymorphic). Twenty two percent of this diversity is distributed *among* populations, influenced to some degree by ecological and life-history factors. Huenneke (1991) notes the ecological significance

of genetic variation within and among populations for microhabitat differentiation, resistance to pathogens and herbivores, and overall ecological amplitude. And Menges (1991) has described the correlation between low genetic variability in populations and increased vulnerability to genetic, environmental, catastrophic and demographic stochastic events.

Although direct experimental confirmation of these assertions remains scattered, genetic variation should be a major factor in designing reintroduction programs (Templeton, 1990). As Holsinger (1991) observes, although the genetic architecture of most rare species has not been studied directly, the existing literature does permit reasonable generalizations. For example, outcrossing species on the whole exhibit a higher proportion of polymorphic loci (p) and more alleles per polymorphic locus (A) than do selfing species; conversely, selfing species distribute a far higher proportion of their variation *among* populations (G_{st}) than do outcrossers. These and other general observations should permit the design of reasonably effective genetic sampling programs, especially given the small number of natural populations for most rare plants. Propagules should be drawn from several populations, and from a sufficient number of individuals within each population, to ensure that the majority of genetic variation at polymorphic loci has been captured. Several sampling strategies have been proposed for rare plants (*see*: Brown and Briggs, 1991; Center for Plant Conservation, 1991; Guerrant, 1992). Reintroduction plans should reflect conscious decisions about the size of reintroduced populations; artificially small populations may be considerably more vulnerable to stochastic events, drift and inbreeding depression, particularly in species that are not adapted to small population size in the wild. Guerrant (1992) observes that many reintroduction programs should involve the establishment of several experimental populations, to guard against environmental and genetic stochasticity, and to exploit microclimatic differences.

Among the major biological considerations in rare plant reintroductions are:

1. What is known about the genetic structure of the species, within and among populations? Can assessment of this variation be built into the project design?
2. What is known about the population biology and demography of the species, including effective breeding popula-

tion size? What short- and long-cycle fluctuations in these values are observed in natural populations?

3. How many experimental outplant sites should there be?
4. From which populations should propagules be drawn? Should genetic material from several populations be combined or kept isolated?
5. Is the species endemic to certain edaphic types? Can it survive elsewhere if competition is controlled? Do the edaphic tendencies appear to be obligatory? Are these observations consistent for all populations?
6. What are the essential symbionts: pollinators, seed dispersants, mycorrhizal fungi, others?
7. What is the species breeding system? Is propagation largely sexual, asexual, mixed, or variable? What is the likelihood that the population will be able to establish itself reproductively on the new site?
8. What are the viability characteristics of the seeds? What dormancy mechanisms exist, and how is dormancy broken? What proportion of the genepool remains as ungerminated seed in the soil seed bank (Glass, 1989)?
9. What are the optimal environmental conditions for seedling growth? How much tolerance does the species have for conditions different from the optima?
10. Is the species characteristic of successional environments? Can it survive elsewhere if competition is controlled?
11. What is the species' "natural" range? What factors, natural and anthropogenic, limit its distribution?

5. Technical Feasibility

Consideration of the finer points of context and strategy will be largely academic if a reintroduction project is not technically possible. Feasibility certainly represents an absolute prerequisite for any actual on-the-ground activity and should be borne in mind throughout the planning process. Nonetheless, we have reserved this section for last because we believe that the feasibility of a project should not necessarily determine its priority or desirability. In other words, simply because reintroduction *can* be done does not mean it necessarily *should* be done.

Technical considerations grade strongly into the basic issues of biology discussed in the preceding step. For instance, lack of

understanding about seed dormancy, pollinators, or edaphic requirements may raise questions about the biology of a project, but such unknowns also create uncertainty about its feasibility. Moreover, short-term success may not mean that long-term technical problems have been solved. For instance, a recent study of California coastal sage scrub indicated that, although there was evidence of scrub seedling regeneration in the first few years of the project, the true success of the reintroduction could not be reliably assessed for 30–50 years. Similar caveats have been raised for community restorations and population reintroductions in prairies, woodlands and riparian areas (*see* essays in Jordan et al., 1987). Technical feasibility of the off-site cultivation phase may also play a part in the planning and reintroduction process for sub-tropical species, as Wallace (1990) has described for sand scrub endemics of peninsular Florida.

A review of reintroduction and restoration literature reveals a wide assortment of technical considerations for successful reintroduction practice. Most considerations are highly specific to a species or habitat type (e.g., Tipton and Taylor, 1984), but a few general considerations emerge as significant:

1. Does a reliable source of reintroduction material exist, either in a natural population or off-site conservation collection? If the latter, are provenance, genetic composition and curatorial history known?
2. If collecting propagules from a wild population is required, do plants exist in sufficient numbers? Is the population reproducing, and if so are seeds or vegetative propagules produced in sufficient quantity to permit removal without interfering with reproduction?
3. Can material be reliably propagated to a stage that permits transplanting? Is there a dormancy requirement before seeds will germinate?
4. Are propagules disease-free? Is there any possibility of importing diseases inadvertently into the new habitat, or if augmenting a population, into existing habitat?
5. Are techniques for transplanting material known? Is there evidence that transplants will survive? What sort of interim management measures, such as watering, will be required in the early stages?
6. Is the recipient site free of threats or disturbances that might

compromise the prospects for success? Is the site stabilized physically from erosion? Is the recipient community invaded by exotic organisms that might reduce the likelihood of success?

CONCLUSION

Increasing destruction, disturbance and fragmentation of remaining pristine habitat require that alternative strategies be sought rapidly and incorporated into strategic planning for biodiversity. Reintroduction and restoration represent important tools for the preservation of biological diversity in its ecological and evolutionary context (Falk, 1992), as well as suggesting a more balanced and creative relationship of human society to nature than industrial societies have achieved to date (Jordan, 1986). It is imperative that practitioners of these important techniques remain clear about the strategic implications of their actions, to ensure that the work of restoration contributes positively to the continuation of the diversity of life on Earth.

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CENTER FOR PLANT CONSERVATION
MISSOURI BOTANICAL GARDEN
P.O. BOX 299
ST. LOUIS, MO 63166

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HYMENOPHYLLUM WILSONII HOOKER (HYMENOPHYLLACEAE) IN THE IBERIAN PENINSULA

F. X. Soñora, S. Ortiz and J. Rodriguez-Oubiña

We found *Hymenophyllum wilsonii* Hooker (SANT 19335) in the basin of the River Seixo de Landoi in the Serra da Capelada (Ortigueira, A Coruña, N.W. Spain; UTM 29TNJ8637; Figure 1). Hitherto, this small fern, which Laínz (1986) included among the *species inquirenda* in the Flora Iberica, in Europe has only been reported in northern and western Great Britain, Ireland, the Faroes, S.W. Norway, N.W. France, Madeira, the Azores and Canaries (Jalas and Suominen, 1972).

The site at which *Hymenophyllum wilsonii* was found is located at an altitude of 350 m a.s.l. on a substrate of serpentines and granulites. According to the chorological typology of Rivas-Martínez (1987), it is in the Eurosiberian region, Cantabro-Atlantic province, Galaico-Asturian sector. The climate, of Atlantic European [V(VI)] type according to Allúe's classification and of temperate maritime type according to Papadakis' (Carballeira et al., 1983), is ideal for this relictual pteridophyte: the annual mean temperature is 12.5°C, the mean annual rainfall 1500 mm, and there are no frosts or summer drought (Giaccobbe dryness index 7). Bioclimatically, this site lies in the hyperhumid ombroclime hill belt of Rivas-Martínez (1987).

Hymenophyllum wilsonii carpets the wet rocks of the watercourse with *H. tunbrigense* (L.) Sm., in a shady, humid environment engendered by a canopy of *Quercus robur* L. This environment likewise harbors other biogeographically interesting ferns of Macaronesian type according to the biogeographical typology of Pichi-Sermolli et al. (1988), including *Vandenboschia speciosa* (Willd.) Kunkel and, in particular, *Culcita macrocarpa* K. Presl. The latter, with specimens exceeding 4 m in height, spreads almost uninterruptedly along the shaded bank of the river over an area of more than half a hectare, making this population certainly the largest known one in continental Europe.

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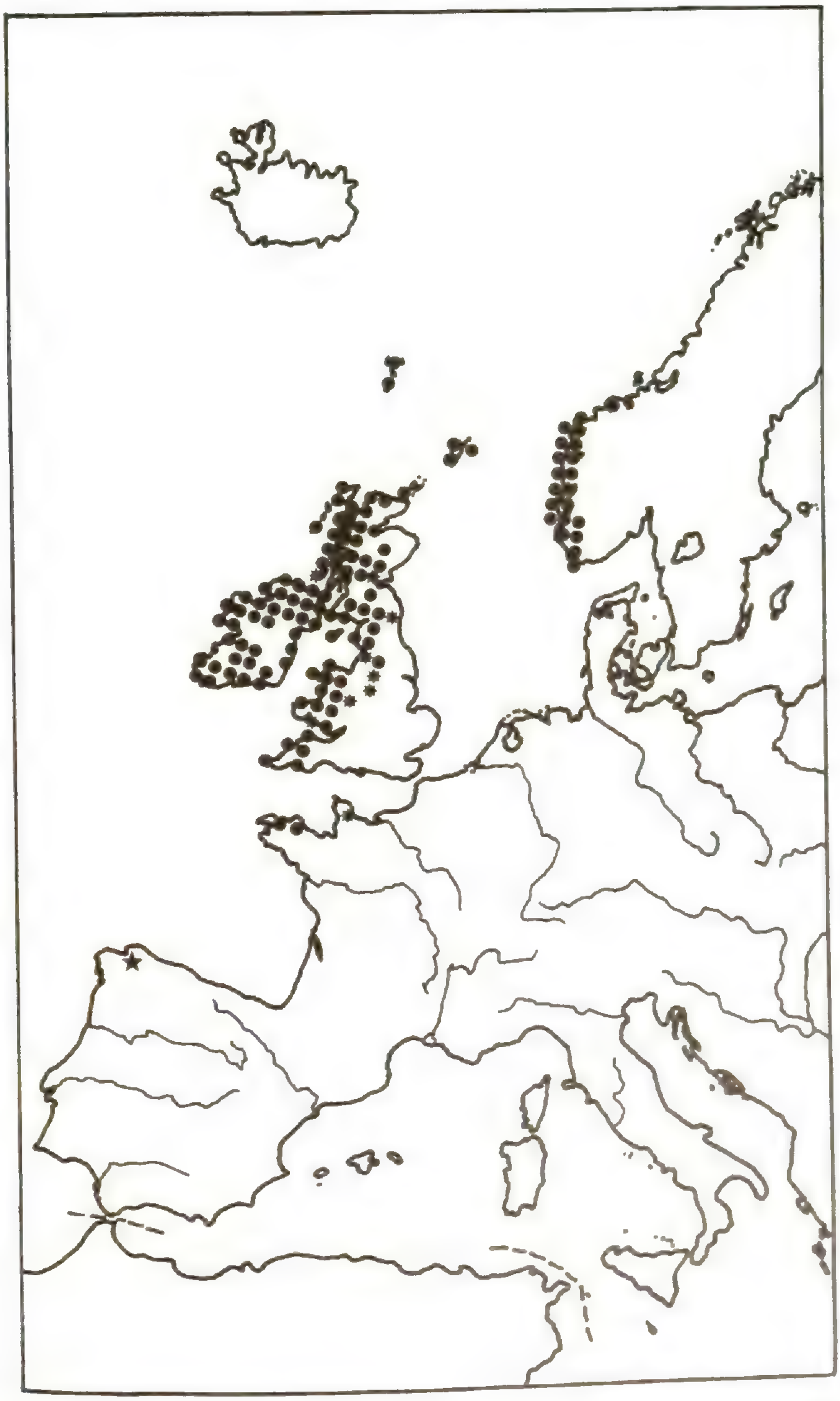

Figure 1. Location of *Hymenophyllum wilsonii* Hooker in continental Europe (Jalas and Suominen, 1972). Native ocurrence: ●: probably extinct: ✸: new locality: ★.

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DEPARTAMENTO DE BIOLOXIA VEXETAL
LABORATORIO DE BOTANICA
FACULDADE DE FARMACIA
UNIVERSIDADE DE SANTIAGO
15706 SANTIAGO DE COMPOSTELA
GALICIA—ESPAÑA

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CHOOSING THE CORRECT NAME FOR *ACONOGONON* (*POLYGONUM* SECT. *ACONOGONON*) IN ALASKA

KENTON L. CHAMBERS

Polygonum alaskanum Wight ex Hultén (1944) represents the earliest validly published name for the species that was called *Aconogonon hultenianum* (Yurtz.) Tzvel. in a recent monograph (Hong, 1991). In many earlier works the authorities for *P. alaskanum* were given as "(Small) Hultén." However, Small should not be cited as the parenthetical author because the latter's earlier-published varietal name *Polygonum alpinum* var. *alaskanum* Small (1895) is an avowed substitute for *P. alpinum* var. *lapathifolium* Cham. & Schlecht., and hence it is illegitimate. The publication by Chamisso and Schlechtendal, however, does provide the description and type for the legitimate new name *P. alaskanum* published by Hultén.

DISCUSSION

Polygonum alaskanum Wight ex Hultén is widespread in Alaska and northwestern Canada. The purpose of this note is to call attention to the legitimacy of the above name (Hultén, 1944), and to correct the nomenclature for this species given in a recently published taxonomic treatment (Hong, 1991).

The taxon in question was first named at the varietal level as *Polygonum alpinum* var. *lapathifolium* Cham. & Schlecht. (Linnaea 3: 38. 1828). Small recognized this variety in his monograph of *Polygonum* in North America (1895), but gave it the new name *P. alpinum* var. *alaskanum* Small, while citing the name by Chamisso and Schlechtendal as a synonym. Small pointed out the prior existence of the species name *P. lapathifolium* L., based on a different type, and he may have been following the precedent of some other taxonomists of his time, who disallowed more than one use of a given epithet within a genus—even at different levels in the taxonomic hierarchy. In any case, the varietal name published by Small is an avowed substitute for the earlier var. *lapathifolium* of Chamisso and Schlechtendal; it is therefore nomenclaturally superfluous and illegitimate under the International Code of Botanical Nomenclature (Greuter, 1988, Art. 63; Kartesz and Gandhi, 1990).

Hultén (1944) was the first to propose a name at the species rank for this taxon. In his publication of *Polygonum alaskanum,* he cited "(Small) Wight nov. comb." as authorities for the name, and he gave "*Polygonum alpinum Alaskanum* Small, Monogr. N. Amer. Spec. Polyg. (1895) p. 33" as the basionym. Hong (1991) cited the authorities for *P. alaskanum* as "(Small) Wight ex Hultén," and he claimed that this name was illegitimate. It is evident from Hultén's publication, however, that his intent was to provide a name at the species level for the taxon that had earlier been named *P. alpinum* var. *lapathifolium* Cham. & Schlecht. He stated (p. 612): "*P. alaskanum* was transferred from variety to species by Wight in the manuscript flora of Alaska by Standley, and I therefore keep this name, although it was not published, especially as the first varietal name of the plant, *lapathifolium,* cannot be used, as it is already occupied" [note: cf. *Polygonum lapathifolium* L.]. Article 41.3 of ICBN (Greuter, 1988) specifies that "In order to be validly published, a name of a species must be accompanied . . . (b) by a reference to a previously and effectively published description or diagnosis of a species or infraspecific taxon. . . ." This requirement is met by Hultén's citation both of "*Polygonum alpinum* γ *lapathifolium* Cham. & Schlecht. in Linnaea 3 (1828) p. 38" and "*Polygonum alpinum Alaskanum* Small, Monogr. N. Amer. Spec. Polyg. (1895) p. 33." A regulation in ICBN which mentions the option of using previously illegitimate epithets in a new position or sense is Art. 72, Note 1: "When a new epithet is required, an author may adopt an epithet previously given to the taxon in an illegitimate name if there is no obstacle to its employment in the new position or sense; the resultant combination is treated as the name of a new taxon or as a *nomen novum,* as the case may be." At the time of Hultén's work, no other specific epithet had been published for this taxon; therefore, Art. 72, which deals with rejected names and *nomina nova,* does not strictly apply. I mention it here as an example of a rule that sanctions the use of illegitimate epithets when forming new names in particular cases.

In his revision of *Aconogonon* (Meisn.) Reichenb. (*Polygonum* sect. *Aconogonon* Meisn.), Hong (1991) rejected the name "*Polygonum alaskanum* (Small) Wight ex Hultén" as illegitimate. Instead, Hong took up *Aconogonon hultenianum* (Yurtz.) Tzvel. (Novit. Syst. Plant Vasc. 24: 77. 1987), which is based on *Polygonum alaskanum* ssp. *hultenianum* Yurtz. (Bot. Zurn. 59: 1452.

1974; type from Fairbanks area, Alaska; collected in 1962). Hong also stated that the synonym *P. alpinum* ssp. *alaskanum* "(Small) Welsh" (1968), with the basionym attributed to Small rather than to Hultén, was illegitimate.

The original publication refers to "*Polygonum alaskanum* (Small) Wight" as a "*nov. comb.*" rather than a "*sp. nov.*" Despite Hultén's choice of phrases, we must retrospectively credit him with having named a new species by reference to a previously published description of the taxon at the varietal level. There appears to be no barrier to the acceptance of *Polygonum alaskanum* Wight ex Hultén as the earliest validly published name for the species.

Polygonum alaskanum is typified by plants of the pubescent phase of the species [to which Hong (1991) gave the name *Aconogonon hultenianum* var. *lapathifolium* (Cham. & Schlecht.) S.-P. Hong]. The usually glabrous, more eastern phase has as its earliest varietal name *P. alaskanum* var. *glabrescens* Hultén (1944). Because I favor use of the generic name *Polygonum* for these taxa, I leave to other workers the option of a new combination placing var. *glabrescens* in *Aconogonon*. The taxonomic assignment of *Polygonum alaskanum* varies in recent floristic works. It was merged with *P. phytolaccifolium* Meisn. ex Small by Hitchcock (1964) and with *P. alpinum* All. by Welsh (1968). The name "*Aconogonon alaskanum* (Small) Wight" mentioned by Hong (1991, p. 331) cannot be traced; however, there does exist the name *Aconogonon alaskanum* (Wight ex Hultén) Sojak [as "(Small) Sojak"], Preslia 46: 150. 1974. The name *Polygonum alaskanum* (Small) Wright [sic!] ex Harshberger (1928) is a *nomen nudum* published without description or bibliographic reference.

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DEPARTMENT OF BOTANY AND PLANT PATHOLOGY
OREGON STATE UNIVERSITY
CORVALLIS, OR 97331

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COMMENTS ON THE PHENOLOGY OF *CARPHEPHORUS CORYMBOSUS* (COMPOSITAE)

DAVID T. COREY

The genus *Carphephorus* includes 4 species (Correa and Wilbur, 1969; King and Robinson, 1987). There is no published information on the phenology of any *Carphephorus* species. This report gives the phenology for *Carphephorus corymbosus* (Nutt.) Torr. & Gray.

Carphephorus corymbosus is a perennial herbaceous composite. Plants of this species consist of an acaulescent rosette of spatulate to oblanceolate leaves from thickened, fibrous roots, and a long green terete stem which branches into an inflorescence with purple to lavender flowers (Correa and Wilbur, 1969). Stems have alternate leaves which become progressively smaller distally.

Carphephorus corymbosus grows in open, sandy areas in sand pine scrub, sandhills, and open pinewood barrens from southeastern Georgia throughout most of peninsular Florida (Correa and Wilbur, 1969; Wunderlin, 1982). The species is an indicator species of sandhills. I examined 3848 basal rosettes at 12 sandhill communities in north and central Florida from 24 August to 8 November 1988 (Figure 1). *Carphephorus corymbosus* was absent from 2 of these study sites (Suwannee River State Park, Suwannee Co. and San Felasco Hammock Preserve, Alachua Co.). Its density at the 10 remaining sites ranged from .004 basal rosettes per m^2 at Wekiwa Springs State Park, Orange Co. to .470 at Spruce Creek Preserve, Volusia Co. (mean = .086 basal rosettes per m^2 for the 10 study sites). Density was determined in late summer and early fall.

Shoots emerge from vertical roots in early March. Each root may produce from 1 to 5 basal rosettes ($\bar{x} = 3$), which arise a few mm below the surface and probably from the root/hypocotyl. These basal rosettes often arise from locations on the rootstock different from those of the previous year. Although 1–5 basal rosettes may be produced, usually only one produces a flowering stem (range: 42.8–136.2 cm, $\bar{x} = 74.9$ cm, $n = 197$; stems were measured only after buds had opened). Rarely, 2 basal rosettes produced stems; in these cases, the second stem was always much shorter than the first. This variation may be an age difference: older rootstocks may produce more basal rosettes and eventually more stems. More research is needed in this area.

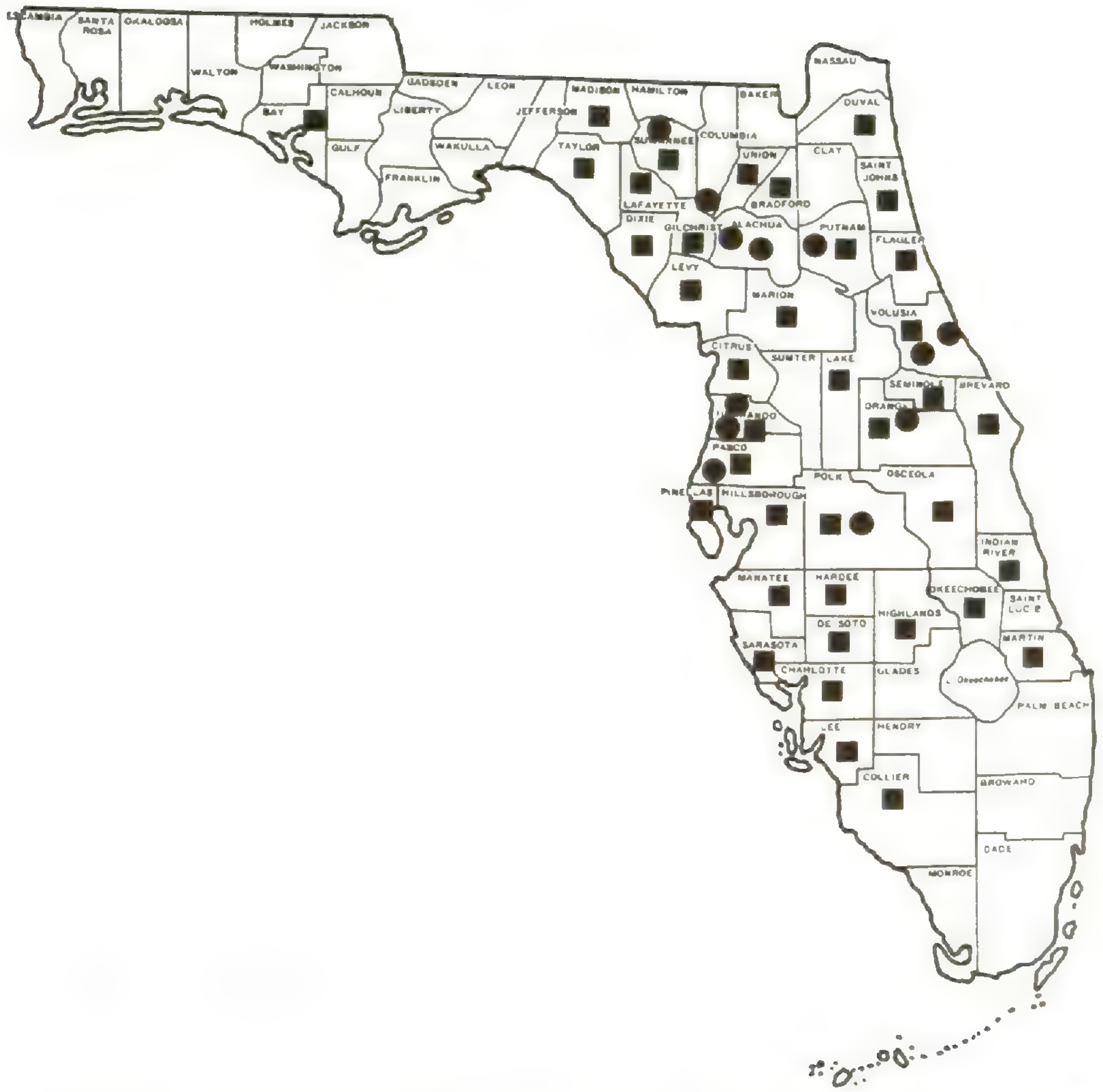

Figure 1. Range of *Carphephorus corymbosus* in Florida (■) and 12 study site locations (●): Suwannee River State Park, Suwannee Co.; O'leno State Park, Columbia Co.; San Felasco Hammock and Morningside Nature Center, Alachua Co.; Interlachen, Putnam Co.; Spruce Creek Preserve and Orange City, Volusia Co.; Wekiwa Springs State Park, Orange Co.; Janet Butterfield Brooks Preserve and Sandhill Boy Scout Reservation, Hernando Co.; Starkey Well Field Area, Pasco Co.; Bok Tower Gardens, Polk Co.

Of the 3848 basal rosettes examined, 9.25% produced inflorescences. Terete stems first appear in late May and reach full length by early June. Around mid-June buds develop on the ends of the corymbs; flowers appear in mid-August. Leaf fall occurs in December and the stems and corymbs dry out but remain standing well into the next year, and often may be seen alongside new basal rosettes with stems. On several occasions, a root mass was dug up (reburied after examination); it bore a new basal rosette with a stem and an old dried stem from the previous year.

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DEPARTMENT OF ZOOLOGY
SOUTHERN ILLINOIS UNIVERSITY
CARBONDALE, IL 62901

THE NEW ENGLAND BOTANICAL CLUB
22 Divinity Avenue
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Vol. 94 October 1992 No. 880

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Cover Illustration

Rhexia virginica L., meadow beauty, is found from Nova Scotia to Georgia, but is rare at the northern limits of its range. The only northern outlier of the tropical family Melastomataceae, it has distinctive 3-veined leaves and geniculate stamens. Original artwork by Josephine Ewing.

Rhodora

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CLIMATE AND THE DISJUNCT DISTRIBUTION OF *POLYSTICHUM ALFARII* (CHRIST) BARR., *COMB. NOV.* IN MESOAMERICA

DAVID S. BARRINGTON

ABSTRACT

Polystichum alfarii (Christ) Barr. is here recognized as a species with a wide disjunction from the montane regions of northern Mesoamerica to the mountains of Costa Rica and Panama. Morphological circumscription and a meiotic chromosome number of $n = 41$ bivalents are provided. Comparison of habitat and distribution with other Central American species of *Polystichum* suggests that the 620 km disjunction of *P. alfarii,* noteworthy for a lower-altitude *Polystichum* species in Mesoamerica, is related to its unique preference for seasonally dry forests at altitudes between 1300 and 1700 m.

Key Words: *Polystichum alfarii,* plant nomenclature, disjunction, biogeography, climate and distribution, Mesoamerica

INTRODUCTION

Polystichum, though not the most diverse fern genus in Latin America, has presented unique problems in recognizing species boundaries. Many of these problems are biological: environmentally induced and developmental variation often obscures evolutionary relationships in the genus (Barrington, 1985). Species unrecognized for strictly historical reasons (taxonomic and nomenclatural) have also made it difficult to understand evolutionary relationships in the genus. In 1980, Alan Smith described a distinctive new species of *Polystichum* from Oaxaca, Mexico, which he named after John Mickel, co-author of the recent fern flora for that region (Mickel and Beitel, 1988). Smith excluded a

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small set of materials that differed from *P. mickelii* A.R. Smith in having a true indusium (A. R. Smith, 1981: 200). Recognition of these materials as a distinct species of the Mexican endemic center, also including a large series of plants from southern Mesoamerica, is the subject of this contribution.

METHODS

The work reported here is based on a morphological analysis of a set of about 60 collections (often represented by one or more duplicates) from the following herbaria: BM, CR, DUKE, F, GH, IJ, MO, NY, UC, US, VT, and YU. Thanks are extended to these herbaria for providing loans of materials for this project. This work was carried out in the course of preparing a treatment of *Polystichum* for the Flora Mesoamericana. In the course of ongoing fieldwork in Costa Rica, I encountered the new species (*P. alfarii*) in two sites in the Valle Central; these sites have made additional work with living plants possible. I have not seen the plant in the field at any Mexican or Guatemalan sites.

In January 1991, I collected a sample of 23 living sporophytes from the Cerro Tablazo population, which served as the material for a report of basic information on chromosome number and behavior in meiosis I. Cytological technique largely followed Barrington, 1990.

RESULTS

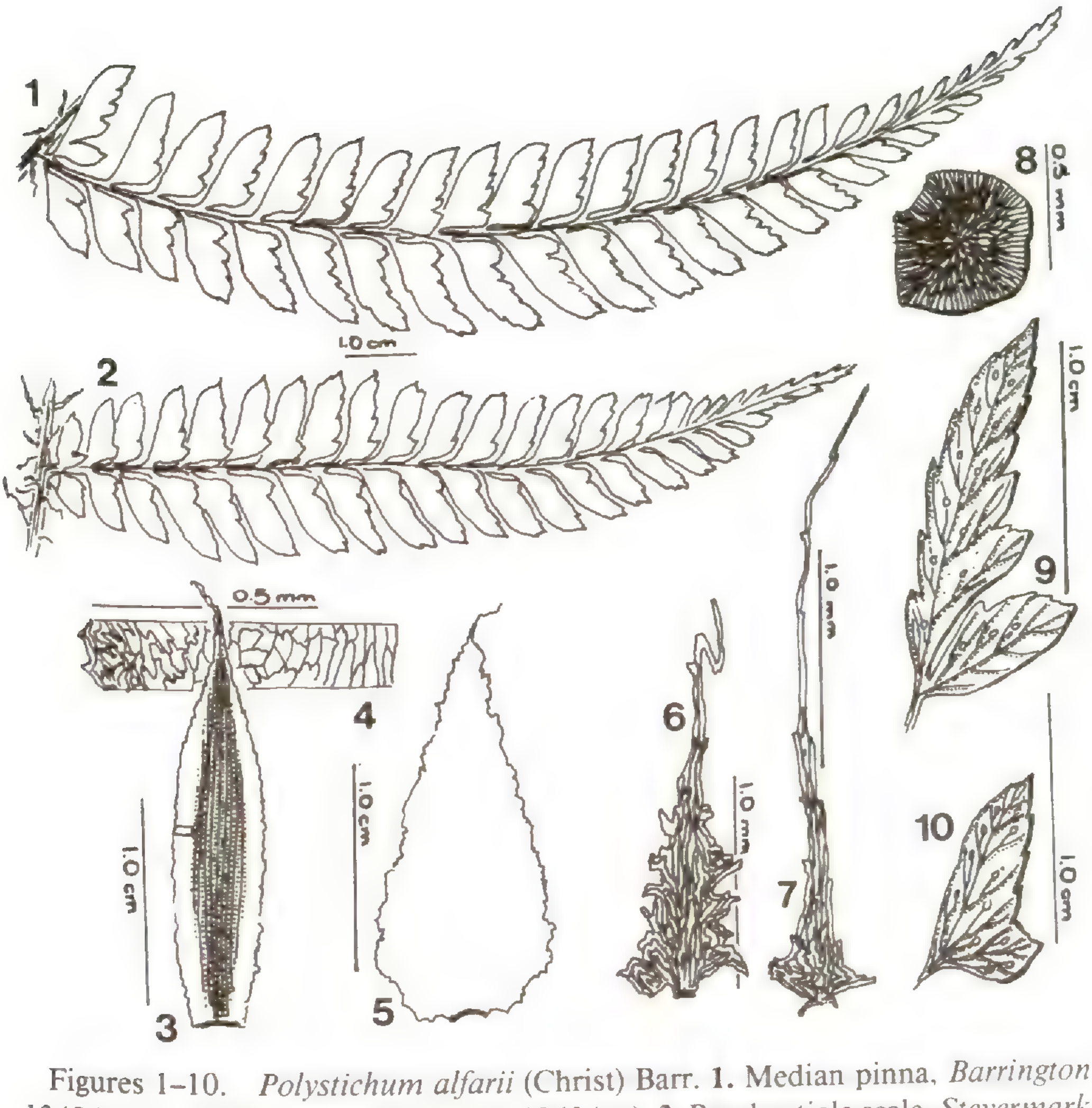
Systematic Section

Polystichum alfarii (Christ) Barr. *comb. nov.* (Figures 1–10)

Polystichum aculeatum (L.) Roth var. *alfarii* Christ, Bull. Herb. Boissier II. 4: 963 (1904). HOLOTYPE: Costa Rica, Alajuelito, 1300 m, March 1902, *Alfaro 16471*, P not seen; ISOTYPE: US!

Polystichum aculeatum (L.) Roth. var. *flavidum* Rosenstock, *Repert. Spec. Nov. Regni. Veg.* 22: 9 (1925). SYNTYPES: Costa Rica, Carthago, 1400 m, 16.IV.1910, *Brade 555*, UC!; Costa Rica, Carpintera, 10.IV.1908. *Brade 26a*, NY!

Rhizome 2–6 cm diam., unbranched; proximal petiole scales lanceolate, center coriaceous, dark reddish brown, border chartaceous, orange-yellow, marginate throughout, the margin irreg-



Figures 1–10. *Polystichum alfarii* (Christ) Barr. **1.** Median pinna, *Barrington 1242* (VT). **2.** Basal pinna, *Barrington 1242* (VT). **3.** Basal petiole scale, *Steyermark 35194* (F). **4.** Detail of edge of basal petiole scale near the center as indicated in Figure 3. **5.** Distal petiole scale, *Steyermark 35194* (F). **6.** Small scale from petiole, *Alfaro 137* (US). **7.** Small scale from pinna-rachis, *Steyermark 35194* (US). **8.** Flange of true indusium from above, *Alfaro 137* (US). **9.** Larger, more dissected pinnule, *Steyermark 35194* (F). **10.** Smaller, less dissected pinnule, *Jiménez 395* (CR).

ular, with a few short rigid to flaccid cilia throughout; distal petiole scales similar, but broad-lanceolate, uniformly papyraceous, orange-yellow or reddish orange with an orange-yellow border, conform or marginate except at base; small scales of petiole mostly ovate-caudate or long-lanceolate (less often deltate or broad-lanceolate), color various but generally dark, marginate at least at base; lamina 37–100+ cm, 2-pinnate-crenate to 2-pinnate-pinnatifid, acuminate; rachis without a proliferous bud, rachis scales light yellowish brown; pinnae 10–16 × 2–2.5 cm, attached at more or less right angles to rachis; pinna-rachis scales filiform or

less often narrow-lanceolate, with a few basal cilia, rare elsewhere; pinnules mucronate, flat, the basal acroscopic pinnules longer than the next distal; veins free, spinules developed only at pinnule tip, weak; sorus round, terminal on vein; true indusium 0.5–0.7 mm diam., irregularly peltate with a margin of narrow, radiate cells and a medulla of regular, slightly elongate cells, most often brownish orange.

The name *Polystichum alfarii* (Christ) Barr. honors Anastasio Alfaro, Costa Rican naturalist and first director of the Museo Nacionál de Costa Rica, who made many important collections in the productive "Golden Age" of work on the flora of Costa Rica (1885–10) (*see* Gómez P., 1977). Alfaro provided early insights into the character of the Costa Rican flora as well as a concise catalog of species (Alfaro, 1887). The type collection, made by Alfaro in March of 1902, is from Alajuelita—now a densely populated suburb just south of San José.

Both Christ and Rosenstock recognized elements of *Polystichum alfarii* from Costa Rica as varieties of *Polystichum aculeatum* (L.) Roth, in keeping with the then popular solution to the problem of recognizing clear species boundaries in the genus *Polystichum*. These varietal names were never consistently applied to *Polystichum alfarii*; the species has most often been left undetermined in herbaria. When collections of *P. alfarii* have been identified, they have been interpreted as any of several species with Mexican affinities, most often *P. ordinatum* (Kunze) Liebm. (a superficially similar species endemic to Mexico and Guatemala), but also as *P. muricatum* (L.) Fée (a remotely allied species occurring sporadically throughout northern Latin American and the Antilles).

A. R. Smith (1981: 200) first drew attention to materials of *P. alfarii* from Chiapas and Guatemala by setting them apart as unnamed collections, which he described as resembling *P. mickelii*. Mickel and Beitel (1988: 315) suggested that this same set of plants from Chiapas and Guatemala might pertain to *P. smithii* Mickel & Beitel, since the two share characters of the indusium and petiole scales. However, *P. smithii* differs from *P. alfarii* in being a much smaller fern with conform (not strongly marginate) petiole scales and fertile pinnules attached at right angles to the pinna-rachis. Judging only from the history of collecting (*see* Appendix), *P. alfarii* is rarer in the northern part of its range. At the

southern limit for the species, the Panama collections of *P. alfarii* have completely escaped recognition until now.

The key features of *Polystichum alfarii* that allow identification are its small (0.5–0.7 mm diam.) but clearly marginate indusium, its strongly marginate but not ovate-caudate or basally thickened petiole scales with dark reddish brown centers and orange-yellow borders, and its lustrous, mucronate pinnules attached obliquely to the pinna-rachis. Most prominent among features varying within the species is lamina dissection. The leaves vary from 2-pinnate crenulate to 2-pinnate pinnatisect, in contrast to most Mesoamerican species, in which leaf dissection of reproductive adults is relatively constant. The complex variation of this species and the superficially similar *P. mickelii* is best represented in a dichotomous key to the two taxa, especially because of the unusual petiole-scale variation in *Polystichum mickelii*.

KEY TO *POLYSTICHUM ALFARII* AND *P. MICKELII*

1. Proximal petiole scales strongly marginate, edge irregular, without superficial cilia, marginal cilia rare, not darkened; distal petiole scales strongly marginate, edge irregular, with a very few short, flaccid cilia; indusium present. 0.5–0.7 mm diam. ..... *P. alfarii*

1. Proximal petiole scales conform or weakly marginate (margin narrow), edge regular, with or without superficial cilia, marginal cilia common, darkened or not; distal petiole scales conform (but isodiametric cells present apically), edge irregular, with many flaccid cilia, sometimes also with short, rigid, dark reddish brown cilia; indusium absent (forms of *P. mickelii*)..... 2

2. Proximal petiole scales without superficial cilia; marginal cilia common, dark reddish brown at least apically; petiole scurf with abundant cilia ... *P. mickelii, typical form*

2. Proximal petiole scales with superficial cilia; marginal cilia rare or absent, pale orange-yellow; petiole scurf with few cilia ..... *P. mickelii, form with superficial cilia*

Ecology

Unlike almost all *Polystichum* species in Mexico and Central America, this species is most common in moist forests, not wet

forests and rain forests (moisture adjectives are used in the quantitative sense of Holdridge, 1967); it has been reported from moist and dry forests and it persists in remnant forests. Among the few *Polystichum* species with a relatively low altitude preference, *P. alfarii* has been encountered between 1140 and 2200 m: about three-quarters of these collections are from between 1300 and 1700 m, with an overall mean altitude of 1540 m. Hence, this species is almost always found below the altitudes where cloud cover itself strongly influences climate (Troll, 1968). Only three out of the 22 species of *Polystichum* known from Mesoamerica (Barrington, 1993) occur at these lower altitudes. A typical *Polystichum, P. alfarii* shows a marked preference for the slopes above streambanks in steep terrain, perhaps indicative of a tendency for gametophytes to pioneer on the moister, unstable slopes near streams. The two study sites where I have seen this species in Costa Rica provide further insight into its ecology and hence its distribution.

At the Cerro Tablazo site above Tablón, in the central valley of Costa Rica (9°50′N, 84°01′W), a large population including plants in numerous size classes occupies an area of at least several hectares in the shade of an evergreen forest at 1600 m, near the median altitude for the species. There, plants are most frequent on very steep (40–60°) slopes in sight of and occasionally at the edge of the swift-moving Río Purires. Younger plants are especially frequent along vertical exposures of bare soil presumably persisting from past stream disturbances and slope wastage at the site. Older plants (often with leaves in excess of 1.5 m long) do not show the same preference for earthen exposures; presumably the disturbances they originally occupied have since been stabilized and obscured.

Climate at the Tablón site is markedly different from that typical of *Polystichum* sites in Costa Rica—Herrera (1985) maps the site as "clima subhumedo, caliente, con una estación seca moderada (35–70 dias con déficit de agua)." The most frequent companion pteridophyte at the Cerro Tablón site is *Anemia phyllitides* (L.) Swartz, a species able to withstand considerable water stress. In contrast, typical Costa Rican sites for *Polystichum* species present much less demanding water-availability regimes. In addition, most sites provide less heat. Herbarium-sheet data suggest that *P. alfarii* is commonly found in regimes such as that encountered at Tablón.

By contrast, I have also seen *Polystichum alfarii* at Porrosatí

(10°06′N, 84°05′W), on the slopes of Volcán Barba, one of the series of volcanoes lying north of the central valley in Costa Rica. There, at the highest site at which the species has been encountered, the species is extremely rare—only one immature individual was seen in January, 1991. The Porrosatí site is a 5 m-deep ravine cut in recent volcanic sediments by the Río Ciruelas, which is surrounded by agricultural land cleared from cloud forest. The plants seen there all grew on the earthern walls of the ravine in deep shade. The poorer performance of this species at this higher, wetter site again suggests that, unlike other Costa Rican species, *P. alfarii* is a plant of drier, warmer forests. These forests, on the gentler lower slopes of the montane regions of the country and near the major population centers, are among those most disturbed by the human population.

Distribution

The most striking feature of *Polystichum alfarii*'s distribution is a range disjunction of 620 km, from the volcanic slopes above San Ramón in Costa Rica to Volcán de San Vicente in El Salvador (Figure 11). Similar disjunctions characterize the Central American distribution of three other *Polystichum* species (Table 1). The distributional hiatus defines two centers of distribution, one northern (Chiapas–El Salvador) and the other southern (Costa Rica–Panama). Also evident is a distribution unique for *Polystichum* along the Pacific (lee) slopes of the two montane regions. The single exception to the Pacific-slope rule is the set of now threatened central-valley populations in Costa Rica, where relatively dry moist-forest conditions are enforced in the lee of a volcanic range.

Cytology

Two plants from the Tablón population yielded counts of $n = 41$ bivalents at Meiosis I prophase (Figures 12, 13). These counts are based on four sporocytes for *Barrington 1976* (VT) and two sporocytes for *Barrington 1991* (VT).

Hybridization

William R. Maxon has collected the hybrid between *Polystichum alfarii* and *P. platyphyllum* (Willd.) Presl, a widespread

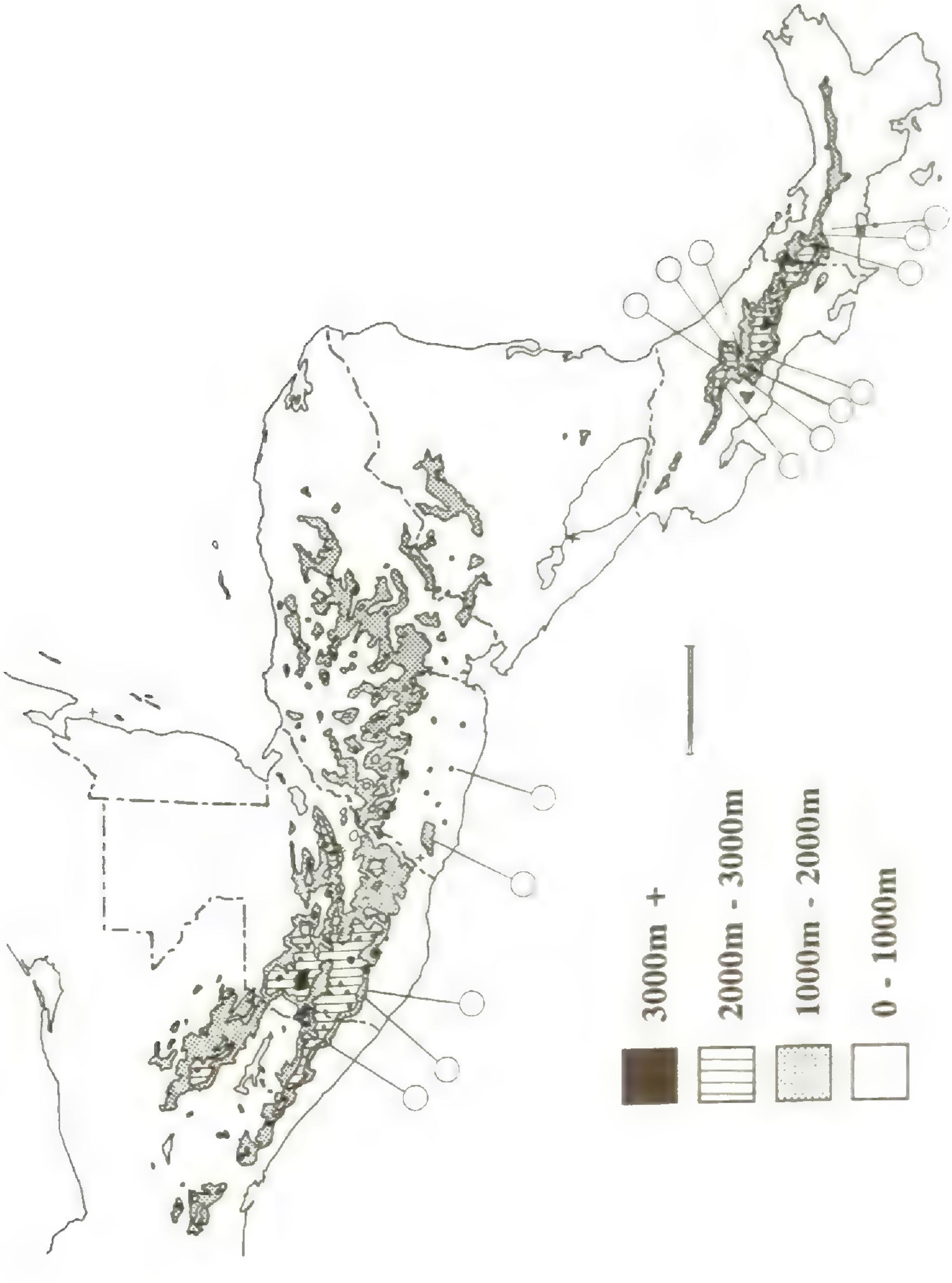
Table 1. Range disjunctions in the widespread Mesoamerican species of *Polystichum* (order is altitudinal range).

Species	Altitudes	Typical Habitat	Maximum Disjunction	Location of Disjunction (or Notes on Range)
P. platyphyllum	600–1500 m	Tropical & premontane wet forests	—	Missing from Guatemala and El Salvador
P. alfarii	1100–2200 m	Premontane moist forest	620 km	El Salvador - Costa Rica
P. muricatum	1100–2700 m	Lower montane wet forest	—	Missing only from El Salvador
P. hartwegii	1200–2700 m	Lower montane wet forest	—	Present throughout Mesoamerica
P. fournieri complex	1900–3100 m	Montane rain forest	550 km	Honduras - Costa Rica
P. speciosissimum	2600–3500 m	High-montane rain páramo	1010 km	Guatemala - Costa Rica
P. orbiculatum	3200–3600 m	High-montane rain páramo	1070 km	Mexico - Costa Rica

exindusiate species of lower-altitude wet and rain forests, from the east end of the Central Valley in Costa Rica. (Collection data: Costa Rica, Pr. Cartago, vicinity of Santiago, humid forest floor, 1050 m, April 20, 1906, *W. R. Maxon, 100,* US 575664!.) This hybrid combines the diagnostic subapical bud and attenuate apex of *P. platyphyllum* with the small indusium of *P. alfarii*. Sporangia of this hybrid rarely open and are largely collapsed. Altitudinally the hybrid is from near the median altitude for *P. platyphyllum* and just below the lowest altitude recorded for *P. alfarii* (Table 1).

→

Figure 11. Distribution of *Polystichum alfarii* (Christ) Barr. Contour intervals are 1000 m. Scale bar is 100 km. Only a few representative collections from the Valle Central of Costa Rica are plotted. Localities are at tip of line opposite the circle.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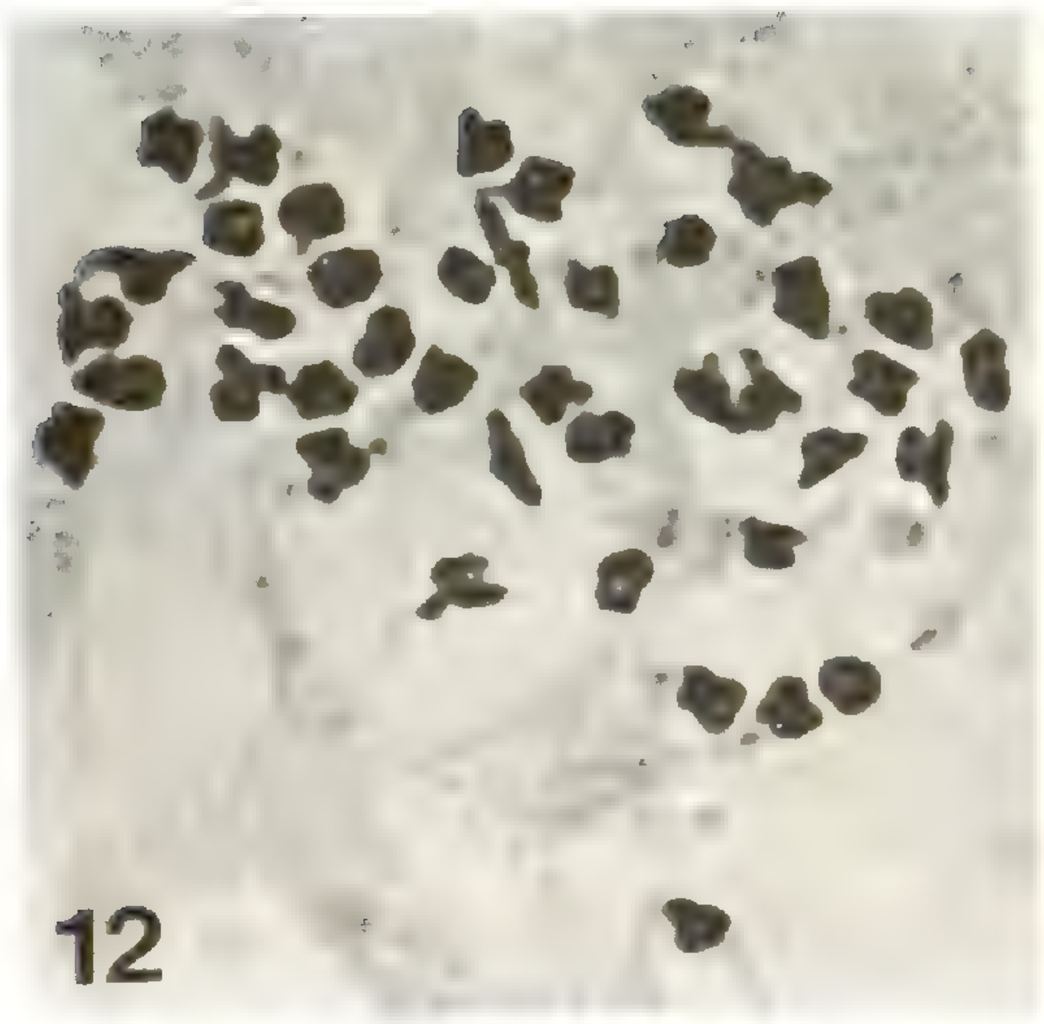

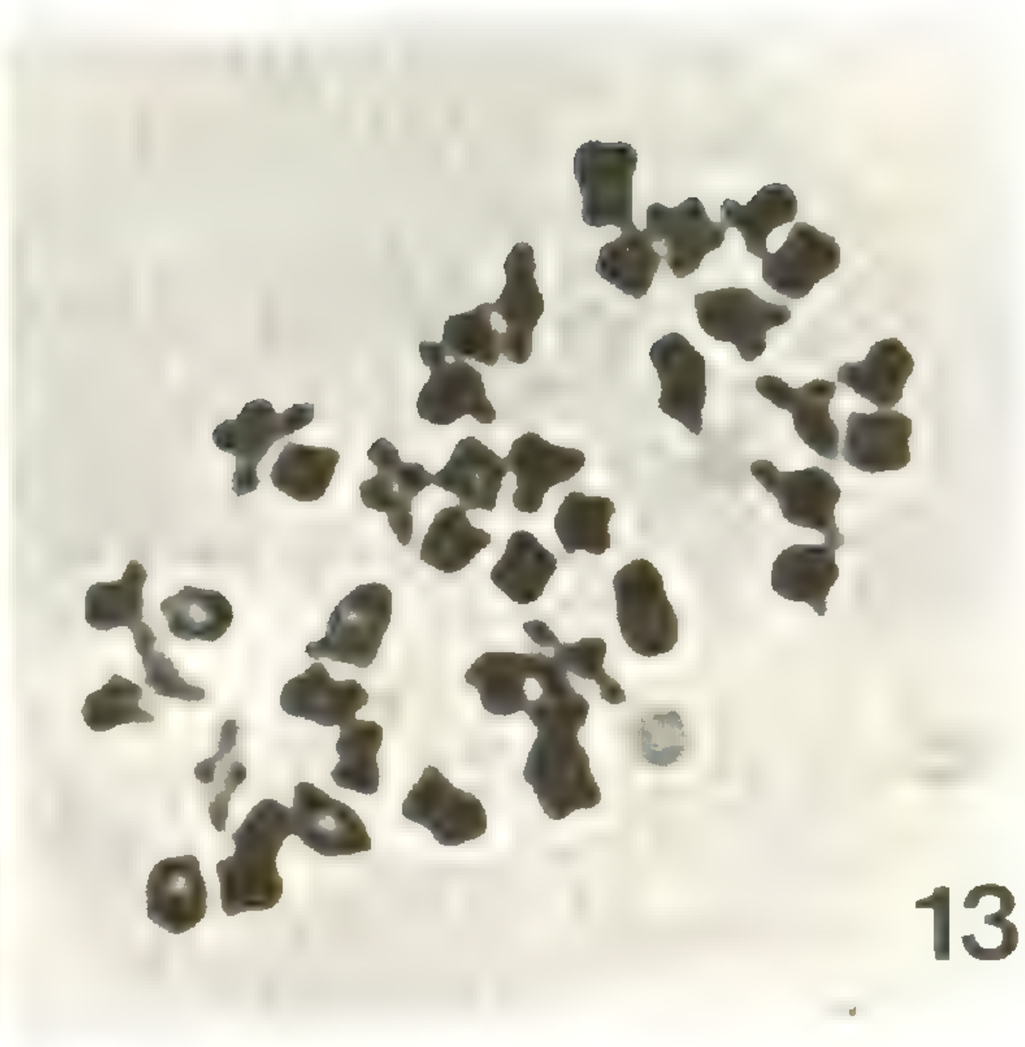

Figures 12 and 13. Meiotic chromosome number for *Polystichum alfarii* (Christ) Barr. Two cells in prophase of meiosis I, $n = 41$ pairs, *D. S. Barrington 1976* (VT).

DISCUSSION

Comparison of the disjunct distributions of Central American *Polystichum* species (Table 1) reveals a relationship between altitude, rainfall regime, and the precise nature of the disjunction. The greatest disjunctions are characteristic of the species with the highest altitude preferences, e.g., *P. orbiculatum* (Remy) Fée and *P. speciosissimum* (Kunze) Tryon & Tryon; both species are confined to alpine or high-montane forest habitats that are limited in distribution in Mesoamerica. In contrast, two species with altitudinal ranges much like *P. alfarii*'s show no significant disjunctions because of the relative continuity of lower montane wet and rain forests where these species are common. *Polystichum alfarii* shows a disjunct distribution like that of evolutionary lineages such as the *P. fournieri* Smith species group from higher (cooler), more island-like montane habitats of Central America, presumably because of its adaptation to drier forests than the other species at equivalent altitudes.

Tryon (1972) portrayed fern species diversity in tropical America in the context of endemic centers. These centers evidence high total numbers of species and high percentages of endemic species; they are separated from others by regions poor in total species and endemic species. Several of his inquiries revealed patterns consistent with an origin of diversity via an evolutionary migration scheme, in which lineages reached different endemic centers

via long-distance dispersal and then diverged from source species in the new region (e.g., *Sphaeropteris*; Tryon, 1971). This scheme is the continental equivalent of inferred histories for insular endemics such as the genus *Diellia* in Hawaii (Wagner, 1952).

Understanding the process by which species diverge in tropical montane regions is dependent on the resolution of species and vicariant species pairs showing disjunct distributions between endemic centers; *Polystichum alfarii* is such a species. More generally, the genus *Polystichum* is of particular interest as a system for the study of the process of evolutionary migration because it is a montane group including a diversity of species with a variety of climatic preferences. The apparent relationship between this variety and geographic distribution suggests that the genus has the potential to provide insight into the determinants of successful diversification in endemic centers.

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APPENDIX

Exsiccatae for *Polystichum alfarii* (Christ) Barr.

MEXICO. **Chiapas:** Finca Irlanda. *C. A. Purpus 7231, 7232* (US), *7243* (GH, MO, US), *7243A* (BM).

GUATEMALA. **Dept. Quetzaltenango:** along Río Samalá, between Santa María de Jesús and Calahuaché, 1200–1300 m, *J. A. Steyermark 33834* (F, US); slopes of Volcán Santa María, 1 mi. below Santa María de Jesús, 1520 m, *J. A. Steyermark 34367* (F); Finca Pirineos, between Santa María de Jesús and Calahuaché, 1350 m, *J. A. Steyermark 35194* (F).

EL SALVADOR: **Pr. Ahuachapán:** Sierra de Apaneca, region of Finca Colima. *P. C. Standley 20135* (GH, US). **Pr. San Vicente:** Volcán San Vicente, 1450 m, *W. Lötschert 84* (US); Volcán San Vicente, *P. C. Standley 21489* (US).

COSTA RICA: **Pr. Alajuela:** La Ventolera, S slope of Volcán Poás, 1700 m, *P. C. Standley 34646* (US). **Pr. Cartago:** Cartago, 1300 m, *A. Alfaro s.n.*, dist. as *J. Donnell Smith 6961* (US); just above Tablón on road up E side of Cerro Tablazo. 1600 m. 9°50′N × 84°01′W, *D. S. Barrington 1242* (CR, VT), *1976, 1991* (VT); Carpintera, 1700 m, *A. Brade & A. C. Brade 26* (GH); Malavassi coffee finca, S of Tres Ríos, 1200 m, *F. M. Givens 3195* (F); in Lankester Garden, 4750′ (native fern), *E. Scamman 5925* (GH); Pacayas, foot of Volcán Turrialba, 1400 m, *E. Scamman 7080* (US); above Tres Ríos, 5000′, *E. Scamman & L. R. Holdridge 7945* (US); Cerro de la Carpintera, 1500–1850 m, *P. C. Standley 34227* (US); Dulce Nombre, 1400 m, *P. C. Standley 35956* (US); La Carpintera, 1800 m, *R. Torres R. 170* (US); Tablazo, 1877 m, *M. Valerio on 8-1-27* (CR 33362); Hacienda Linda

Vista, just S of Dulce Nombre de Culmi, SE of Cartago, 1300 m, *E. J. Judziewicz 4370* (CR, MO). **Pr. Herédia:** 1.7 km NNE of Porrosatí, on the Río Ciruelas, 2200 m, 10°06′N × 84°05′W, *D. S. Barrington 1213* (CR, VT). **Pr. San José:** Río Herradura, tributary of the Río Chirripó del Pacífico, NW of Canaán, General Valley, 1600 m, 9°29′N × 83°37′W, *W. C. Burger & R. L. Liesner 7084* (CR, F); Hacienda La Verbena, Río Tiribí, Alajuelita, 1140 m, *O. Jiménez L. 395* (CR, US). Rio Torres: San Francisco de Guadalupe, *O. Jiménez 360* (CR), San Francisco de Guadalupe, 1150 m, *H. Pittier 7153* (CR, US), *7155* (CR); Cerro de Piedra Blanca, above Escasú, *P. C. Standley 32501, 32533* (US); San Francisco de Guadalupe, *A. Tonduz 9837* dist. as *J. Donnell Smith 7216* (GH, US); El Copey, Río Pedregoso, 1800 m, *A. Tonduz 11853 p.p.* (CR; the US collections of this number are *P. concinnum* Lellinger ex Barr.).

PANAMA. **Pr. Chiriquí:** vic. "New Switzerland," central valley of Río Chiriquí Viejo, 1800–2000 m, *P. H. Allen 1334* (US); Guadalupe, Cerro Punta, 2000 m, *R. Caballero 149* (MO); between Holcomb's trail and Mouniche plantation, above El Boquete, 1500–1725 m, *E. P. Killip 5086* (US); Piedra de Lino, El Boquete, 1400–1600 m, *E. P. Killip 5410* (US); N side of Río Caldera, Horqueta - Bajo Mano, NW of Boquete, *J. L. Luteyn 4581* (DUKE); above Sabana de El Salto, trail to Camp Aguacatal, E slope of Volcán Chiriquí, 1500–1750 m, *W. R. Maxon 5267* (US); km 10.7 on Volcán–Cerro Punta Rd., *G. R. Proctor 32005* (IJ).

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A NATURALLY-OCCURRING POPULATION OF PUTATIVE *ARISAEMA TRIPHYLLUM* SUBSP. *STEWARDSONII* × *A. DRACONTIUM* HYBRIDS IN MASSACHUSETTS

LAURIE L. SANDERS AND C. JOHN BURK

ABSTRACT

A population of putative hybrids between *Arisaema triphyllum* (L.) Schott subsp. *stewardsonii* (Britt.) Huttleston and *A. dracontium* (L.) Schott (Araceae) was found in a disturbed floodplain forest in Hampshire County, Northampton, MA in late spring, 1988. The hybrids are intermediate between the parental species in leaflet number, spadix length, spathe length, and somatic chromosome number. They also exhibit apparent hybrid vigor and occur in a near-classic example of a hybrid habitat.

Key Words: Natural hybrid, *Arisaema triphyllum* subsp. *stewardsonii*, *A. dracontium*, intermediacy, hybrid vigor, hybrid habitat, Hampshire County, Massachusetts

INTRODUCTION

A population of apparent hybrids between *Arisaema triphyllum* (L.) Schott subsp. *stewardsonii* (Britt.) Huttleston and *Arisaema dracontium* (L.) Schott (Araceae) was encountered in June, 1988, in the course of a distributional study of *Arisaema dracontium* (Sanders, 1989). The putative hybrids were identified by leaf types and spadix lengths that are intermediate between those of *A. triphyllum* subsp. *stewardsonii* and *A. dracontium*. The hybrids tended to be taller than plants of either putative parent and were morphologically unique. Both *A. triphyllum* subsp. *stewardsonii* and *A. dracontium* were present and flowering in the immediate vicinity.

Arisaema triphyllum subsp. *stewardsonii* is one of the three major subspecies of eastern North American jack-in-the-pulpits that comprise the *Arisaema triphyllum* complex (Huttleston, 1948, 1949, 1953; Kartesz and Kartesz, 1980; Treiber, 1980.) It has one or two trifoliolate leaves, prominent ridges or fluting on the outer spathe, and a cylindrical spadix that is enclosed within the spathe. The throat of the spathe is marked with green, whitish, or purple-maroon striping and the spadix is pale-green or purplish-maroon.

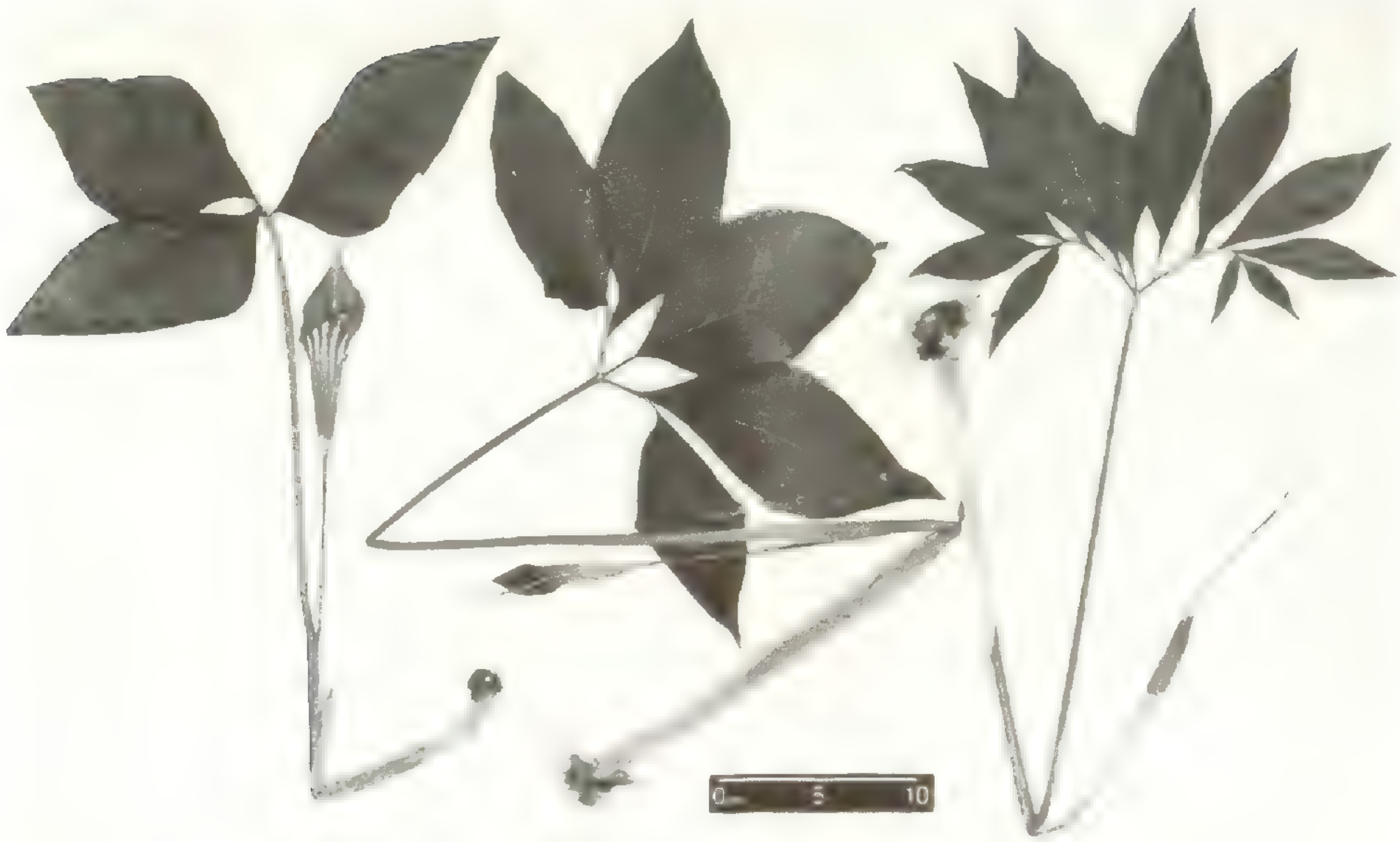

Figure 1. Representative specimens: *Arisaema triphyllum* subsp. *stewardsonii* (left), a putative hybrid (center), and *A. dracontium* (right) collected June, 1988.

Arisaema dracontium, green dragon, has a single pedately 7–17 foliolate leaf, a smooth spathe, and a relatively lengthy, exserted slender spadix (Huttleston, 1948, 1953). The spathe is uniformly lime-green in color and the spadix bright yellow.

The apparent *Arisaema* hybrids are distinguished by their single pedately 5–7 foliolate leaves and their spadix lengths, which are intermediate between the shorter spadices of *A. triphyllum* subsp. *stewardsonii* and the longer ones of *A. dracontium* (Figure 1). Their outer spathes are purplish green and the inner spathes patterned with green and maroon; their spadices are yellow-green with maroon checkering.

Although *Arisaema triphyllum* subsp. *stewardsonii* and *A. dracontium* occur sympatrically throughout much of the northeast portion of their ranges (Huttleston, 1948, 1953), reports of natural hybridization between any subspecies of *A. triphyllum* and *A. dracontium* are virtually nonexistent. Thompson (1911) described a colony of *A. triphyllum* growing in a central Connecticut swamp that "showed peculiarities that suggested its close relationship to *A. dracontium.*" The plants had a strict growth habitat, slender spathes that were atypically erect at their summits, and five-parted leaves. Huttleston (1948, 1953), working near Varna, New York,

observed a number of plants of *A. triphyllum* which possessed slender spathes that were held more erect than usual and lateral leaflets that tended to be lobed, sometimes to the midrib. He concluded that this variation may possibly have resulted from past hybridization with *A. dracontium,* but that present evidence for this was unconvincing. Similarly, Pittillo et al. (1972) noted that a previous report of *A. dracontium* from Henderson Co., NC represented "a peculiar form (possibly a hybrid) of *A. triphyllum.*"

Records of artificial crosses between *Arisaema triphyllum* and *A. dracontium* are limited to brief mentions of artificial hybrids by MacDougal (1901) and Rennert (1902), both of whom describe the germination and seedling characteristics of the parent species but do not describe either how the hybrid cross was made or the appearance of the mature hybrid.

The purpose of the present study is to characterize the floodplain site at which probable hybridization occurred, to describe the putative hybrids more fully, and to compare the hybrids with nearby plants of *Arisaema triphyllum* subsp. *stewardsonii* and *A. dracontium.*

THE STUDY SITE

The population of putative hybrids, which totals approximately 800 plants, occurs within a narrow, two hectare strip of floodplain forest along the Connecticut River in Northampton, Hampshire Co., MA. The hybrids occur together in clusters of 10–20 flowering culms, often accompanied by an equal number of depauperate vegetative stems, at elevations that are normally flooded several times per year. The underlying soils are Pootatuck fine sandy loam and Limerick silt loam (Swenson, 1981). An additional population containing approximately 1000 putative *Arisaema* hybrids was discovered during summer, 1992 in a similar floodplain forest about 1 km distant from the original site.

The study site has been severely affected by natural disturbances, including the formation of an oxbow on the main stem of the Connecticut River in 1840, and by human activities, including the rerouting of an adjacent tributary of the Connecticut River as early as 1710 (Robinton and Burk, 1971; Holland and Burk, 1982, 1984). Railroad and highway constructions have also occurred in the vicinity, and agricultural activities continue on land adjacent to the study site.

The forest canopy at present is dominated by silver maple (*Acer saccharinum* L.). Other trees and shrubs present include *Populus deltoides* Marsh., *Salix nigra* Marsh., *Ulmus rubra* Muhl., *Cornus amomum* Mill., *Fraxinus americana* Marsh. and *Sambucus canadensis* L.

At the time the *Arisaema* populations are flowering, the herbaceous stratum is relatively undeveloped; however, by August both the hybrids and their putative parents are overtopped by surrounding herbs and vines. Prominent associates are *Osmunda claytoniana* L., *Matteucia struthiopteris* (L.) Todaro, *Onoclea sensibilis* L., *Iris pseudacorus* L., *I. versicolor* L., *Boehmeria cylindrica* L., *Laportea canadensis* (L.) Wedd., *Ranunculus abortivus* L., *Amphicarpa bracteata* (L.) Fern., *Vitis* spp., *Rhus radicans* L., and *Arctium* sp.

MATERIALS AND METHODS

During June, 1988 and June, 1989, morphological data were collected from 147 flowering specimens of the putative hybrids and from both *Arisaema triphyllum* subsp. *stewardsonii* and *A. dracontium* in their immediate vicinity. Only 40 individuals of *A. triphyllum* subsp. *stewardsonii* were present and all of these were sampled. *Arisaema dracontium* was abundantly scattered throughout the area and 100 individuals occurring within ten meters of the hybrids were selected for sampling. Representative specimens of all taxa studied are deposited in SCH.

Five character states were recorded from each plant: (1) height from the soil level to the rachis, (2) number of leaves and leaflets, (3) spathe length, including tube and blade, (4) length of the spadix appendage, and (5) gender, whether staminate, carpellate, or monoecious. To avoid damaging the spathe, the spadix appendage was measured from the point at which it exited the spathe to its terminus. Character means between parents and hybrid populations were compared using ANOVA-Fisher Protected Least Significant Difference for pre-planned comparisons (Snedecor and Cochran, 1980).

Observations of post-flowering events, including fruit maturation, were made during June and August, 1988. Pollen morphology was observed from bulk pollen samples collected in June, 1989, from four flowering hybrids and from four plants of each putative parent species. Somatic chromosome counts were ob-

tained from root tips of hybrids and parental species collected in May, 1990. Root tips were treated with 6N HCL for 10 minutes at room temperature, rinsed with distilled water, and then stained with Schiff solution. The materials were then fixed in a 3:1 mixture of absolute alchohol and 45% glacial acetic acid and squashed (technique suggested by Graham Kent, pers. comm.).

RESULTS AND DISCUSSION

HEIGHT TO RACHIS. Although height ranges of the three taxa overlapped, the average height of the hybrids was significantly greater than that of the parental taxa (Table 1).

LEAF AND LEAFLET NUMBER. Plants of *Arisaema triphyllum* subsp. *stewardsonii* had either one or two leaves which were in all cases trifoliolate. All plants of *A. dracontium* and nearly all plants of the putative hybrids had a single pedately-foliolate leaf. During the 1988–90 growing seasons, only three hybrid plants with two leaves were observed. Leaflets per leaf, usually odd in number, ranged from 7 to 17 for *A. dracontium* and from 5 to 7 for the putative hybrids. Differences in leaflet number among the three taxa were significant to the 95% confidence interval (Table 1).

SPATHE LENGTH. Spathe lengths of the putative hybrids were significantly different from either parent. Spathes of the putative hybrids were intermediate in length between the longer spathes of *Arisaema triphyllum* subsp. *stewardsonii* and the shorter spathes of *A. dracontium* (Table 1).

LENGTH OF SPADIX APPENDAGE. Spadices of the putative hybrids were significantly different in length from either parent. Spadices of the putative hybrids were also intermediate in length between the shorter spadices of *Arisaema triphyllum* subsp. *stewardsonii* and the longer spadices of *A. dracontium* (Table 1).

GENDER. Inflorescences of *Arisaema triphyllum* subsp. *stewardsonii* were staminate, carpellate, or monoecious; those of *A. dracontium* and the putative hybrids were either staminate or monoecious.

POST-FLOWERING DEVELOPMENT. Staminate culms of both the hybrids and their putative parents had withered and collapsed by late June, 1988, shortly after flowering. Carpellate and monoecious specimens of *Arisaema triphyllum* subsp. *stewardsonii* and *A. dracontium* remained vigorous and developed fruits through

Table 1. Comparisons between (1) means of height, number of leaflets, spathe length, and length of spadix appendage, (2) gender, and (3) somatic chromosome number for *Arisaema triphyllum* subsp. *stewardsonii, A. dracontium,* and their putative hybrids. (See text for sample numbers and sampling methods).

Character	*A. triphyllum* subsp. *stewardsonii*	Hybrid	*A. dracontium*
Height to rachis (cm)	42.60* (SE = 1.81)	59.17 (SE = 1.13)	42.97* (SE = 0.98)
Number of leaflets	3.00* (SE = 0.00)	5.84 (SE = 0.08)	11.39* (SE = 0.22)
Spathe length (cm)	10.88* (SE = 0.24)	7.79 (SE = 0.11)	5.56* (SE = 0.10)
Length of spadix appendage (cm)	0.00* (SE = 0.00)	3.87 (SE = 0.06)	12.76* (SE = 0.27)
Gender	monoecious staminate carpellate	monoecious staminate	monoecious staminate
Somatic chromosome number	28	42	56

* Significant at 95%.

August. Single immature fruits occurred on a few of the hybrid plants, but by August, 1988, most of the monoecious hybrid culms had collapsed, their pedicels and infructescences withered and dried out. Subsequent observations indicated that no hybrid fruits matured. Vegetative reproduction of the hybrids by production of cormlets, however, was observed; in one instance, a cormlet from a hybrid plant was found approximately one meter downslope from the parent corm.

POLLEN MORPHOLOGY. When examined at a magnification of 43×, pollen grains of both parental taxa were normal in appearance with spherical, well-filled pollen grains. while those of the putative hybrids were found to be malformed and/or collapsed.

SOMATIC CHROMOSOME NUMBER. The somatic chromosome number of *Arisaema triphyllum* subsp. *stewardsonii* from the study site was 56; that of the hybrid was 42, and that of *A. dracontium* 28 (Table 1). Huttleston (1948, 1949, 1953) reported somatic chromosome counts of 28 for *A. triphyllum* subsp. *stewardsonii* and somatic counts of 56 and 28 for *A. dracontium.* A count of 42 for the putative hybrids was also reported by J. Murata (pers.

comm., 1989), who collected three live specimens from the study site in 1988 and determined somatic chromosome numbers from these plants in 1989.

Stace (1980) suggested five criteria that can be used to determine the likelihood that a given plant may be a hybrid. These criteria include (1) phenetic intermediacy between the putative parents, (2) reduced fertility, (3) F-2 segregation, (4) distributional evidence—i.e., proximity of the putative parents to the hybrid, and (5) artificial resynthesis. The putative *Arisaema triphyllum* subsp. *stewardsonii* × *A. dracontium* hybrids examined in the present study easily meet the first, second and fourth of these criteria. Moreover, they occur in a near-classic example of a "hybrid habitat" (Anderson, 1949). In addition, their chromosome number, intermediate between that of a diploid *A. triphyllum* subsp. *stewardsonii* and a tetraploid *A. dracontium,* suggests they represent an essentially sterile triploid cross and that Stace's third criterion, F-2 segregation, would be unlikely in nature.

Given the broad overlap of the ranges of *Arisaema triphyllum* subsp. *stewardsonii* and *A. dracontium* in the northeastern United States, the vigor of the Northampton floodplain hybrids, the number of hybrid plants occurring at the site and their distinctive, clearly recognizable, intermediate morphologies, it remains unclear why the cross has not been reported more frequently.

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DEPARTMENT OF BIOLOGICAL SCIENCES
SMITH COLLEGE
NORTHAMPTON, MA 01063

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THE ASTERACEAE OF THE GUIANAS, III: VERNONIEAE AND RESTORATION OF THE GENUS *XIPHOCHAETA*

HAROLD ROBINSON

ABSTRACT

The tribe Vernonieae is surveyed in continuation of the preliminary reviews of the Asteraceae of the Guianas (Guyana, Suriname, Cayenne), South America. Nineteen species are listed in 15 genera. The genus *Xiphochaeta* is resurrected from the synonymy of *Stilpnopappus* for the northern South American species commonly known as *S. viridis*. Elongate raphids in the achene are emphasized as a character relating *Xiphochaeta* to *Lepidaploa*.

Key Words: Asteraceae, Vernonieae, pollen, *Xiphochaeta*, Guianas, South America

The Flora of the Guianas project has been generally described by Funk (1991) in the first of a series of preliminary reviews of the family Asteraceae in that area. Her 1991 paper treated the tribe Heliantheae while a second study is projected for tribes Anthemideae, Astereae, Lactuceae, Cynareae, Mutisieae, and Senecioneae. The original intent was to treat the Eupatorieae and Vernonieae together in a third paper, but special needs of the Vernonieae have led to a decision to treat that tribe here, separately.

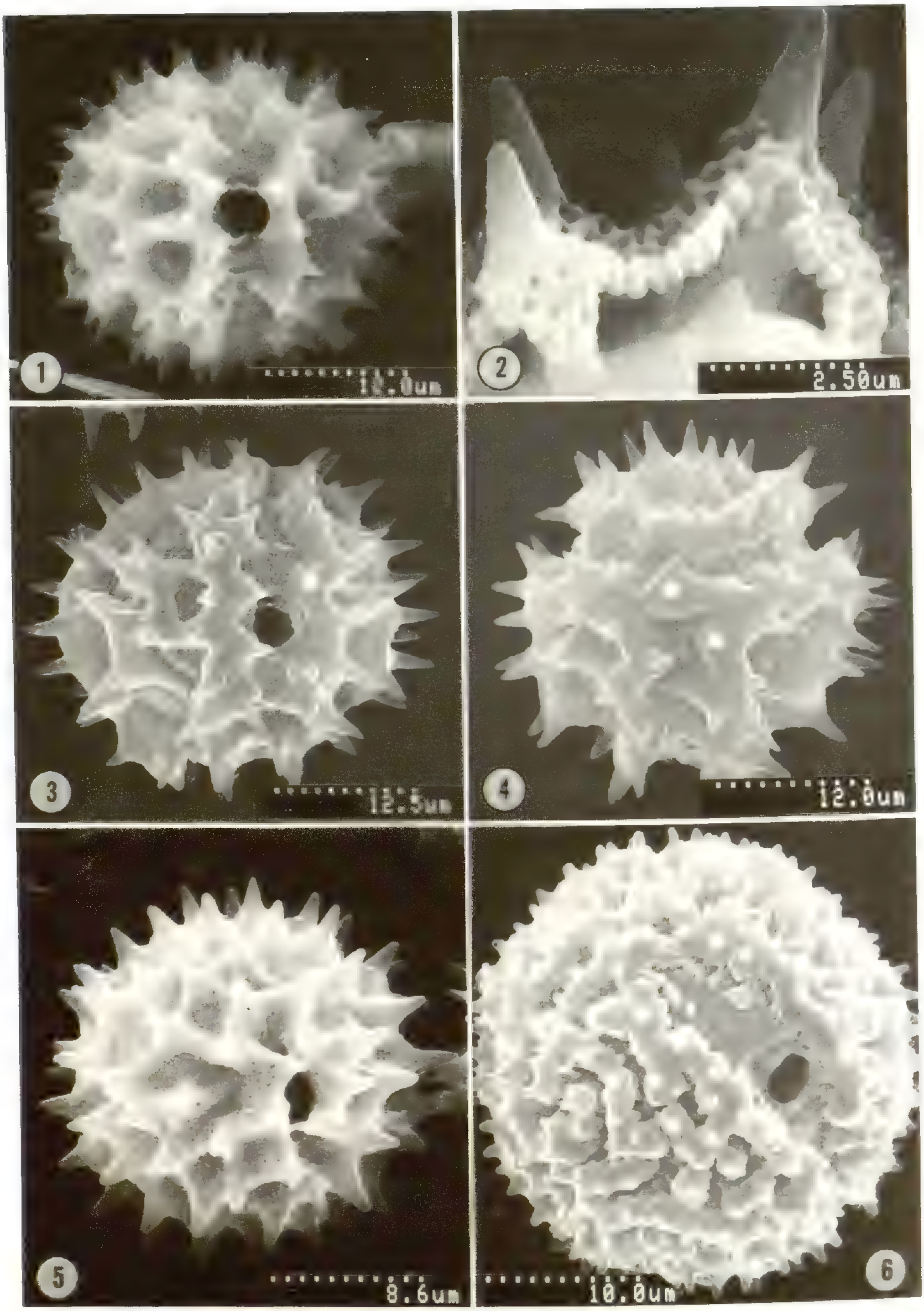
A key to the genera and a list of the species of the Vernonieae is provided as in other preliminary studies. However, the present study is the first to use many recent generic segregates of the Vernonieae in a floristic work. These recent generic segregates, plus a genus resurrected here from synonymy, and previously accepted genera are all keyed in greater detail than usual. Features of the pollen are particularly useful in the Vernonieae, and details of pollen structure are included in the key.

I have dealt with many segregates of traditional *Vernonia* Schreb. in a number of papers. Four of these papers, those dealing with *Cyrtocymura* H. Robinson (Robinson, 1987), *Lepidaploa* (Cass.) Cass. (Robinson, 1990b), *Vernonanthura* H. Robinson (Robinson, 1992), and the introduced paleotropical *Cyanthillium* Blume (Robinson, 1990a), include species in the Guianas. An additional genus, *Xiphochaeta* Poeppig in Poeppig and Endlicher, is restored here for the single species *X. aquatica* Poeppig that is commonly

known as *Stilpnopappus viridis* Benth. ex Baker, occurring in the Guianas and in the Orinoco and northern Amazon basins. The sample of Vernonian neotropical genera occurring in the area is limited, but an initial attempt to use the segregates and the pollen types in a flora is considered important.

Pollens are particularly interesting in the Vernonieae. Pollen variations are numerous and striking (Stix, 1960; Kingham, 1976; Keeley and Jones, 1977) and some of the variations were noticed and used taxonomically as early as the work of Steetz in 1864. The work of Steetz was cited by Bentham and Hooker (1873), but use of pollen as a taxonomic character in the Vernonieae was allowed to lapse almost completely for over a hundred years. This lapse in use of pollen as a character coincided with the period of entrenchment of an excessively broad concept of the genus *Vernonia.* More recently, pollen is one of a series of characters such as style bases and anther appendages, observable with the compound microscope, that prove useful in delimiting natural groups in the Vernonieae. The point has been reached where I believe every taxonomic treatment in the Vernonieae should include mention of pollen type (Robinson, 1988). To aid in use of pollen, SEM illustrations are provided, but almost all the taxonomically important features, such as patterns of muri, colpi, spines and completeness of tectum, can be observed easily with the compound microscope.

General terminology used for various pollen types in the Vernonieae dates initially from Keeley and Jones (1977) and Jones (1981), with elaborations by Robinson (1988, 1990b). Type A is tricolporate and spinose with a perforated tectum continuous over all non-colpar areas (Figure 2). In spite of some variations within the Type A, no formal subdivisions have been established, and only some of the genera with Type A pollen are shown here (*Centratherum, Cyrtocymura,* and *Trichospira*; Figures 1–5). A modified Type A in *Orthopappus* has numerous irregularly crowded muri with narrow areas of discontinuous perforated tectum between (Figure 6). Type B, which is not found in the Guianas, is tricolporate and lophate with distinct areoles, the perforated tectum is restricted to the muri, there are three equatorial areoles between the colpi, and the muri are attached to the footlayer by large baculae. Type C, seen in the Guianas in *Lepidaploa,* is tricolporate and lophate with tectum restricted to the muri; there are two equatorial areoles between the colpi, there is a polar areole,

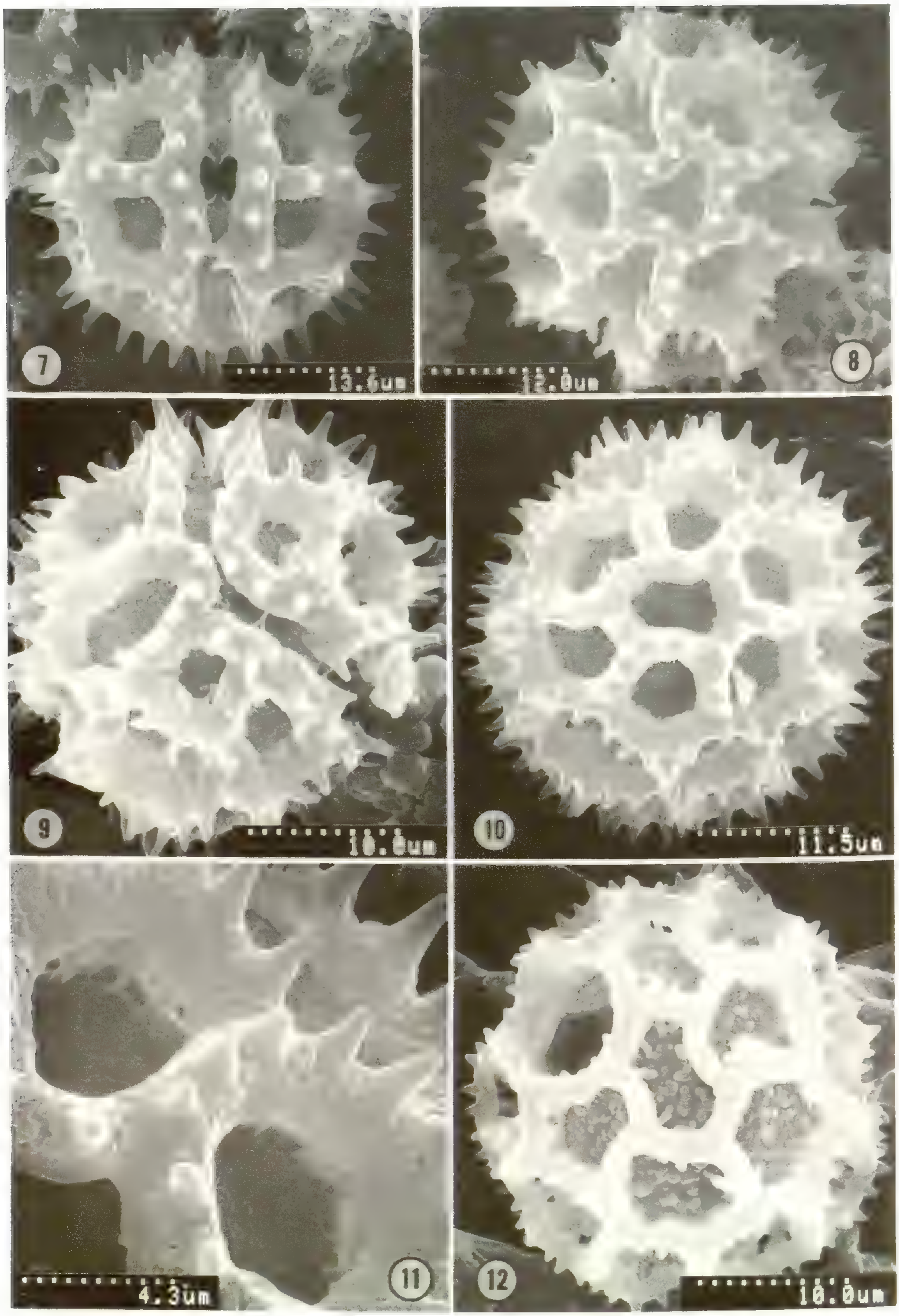


Figures 1–6. Pollens of Guiana Vernonieae, tricolporate, Type A. **1, 2.** *Centratherum punctatum* Cass., Brazil, *Irwin 27191* (US): **1.** colpar view showing pore. **2.** broken grain showing continuous perforated tectum between spines. **3, 4.** *Cyrtocymura scorpioides* (Lam.) H. Robinson, Brazil, *Beetle 2029* (US): **3.** colpar view. **4.** polar view. **5.** *Trichospira verticillata* (L.) Blake, Venezuela, *Velez 2638* (US), equatorial view showing colpus and part of intercolpus. **6.** *Orthopappus angustifolius* (Sw.) Gleason, Bolivia, *Buchtien 785* (US), oblique view showing colpus and part of intercolpus.

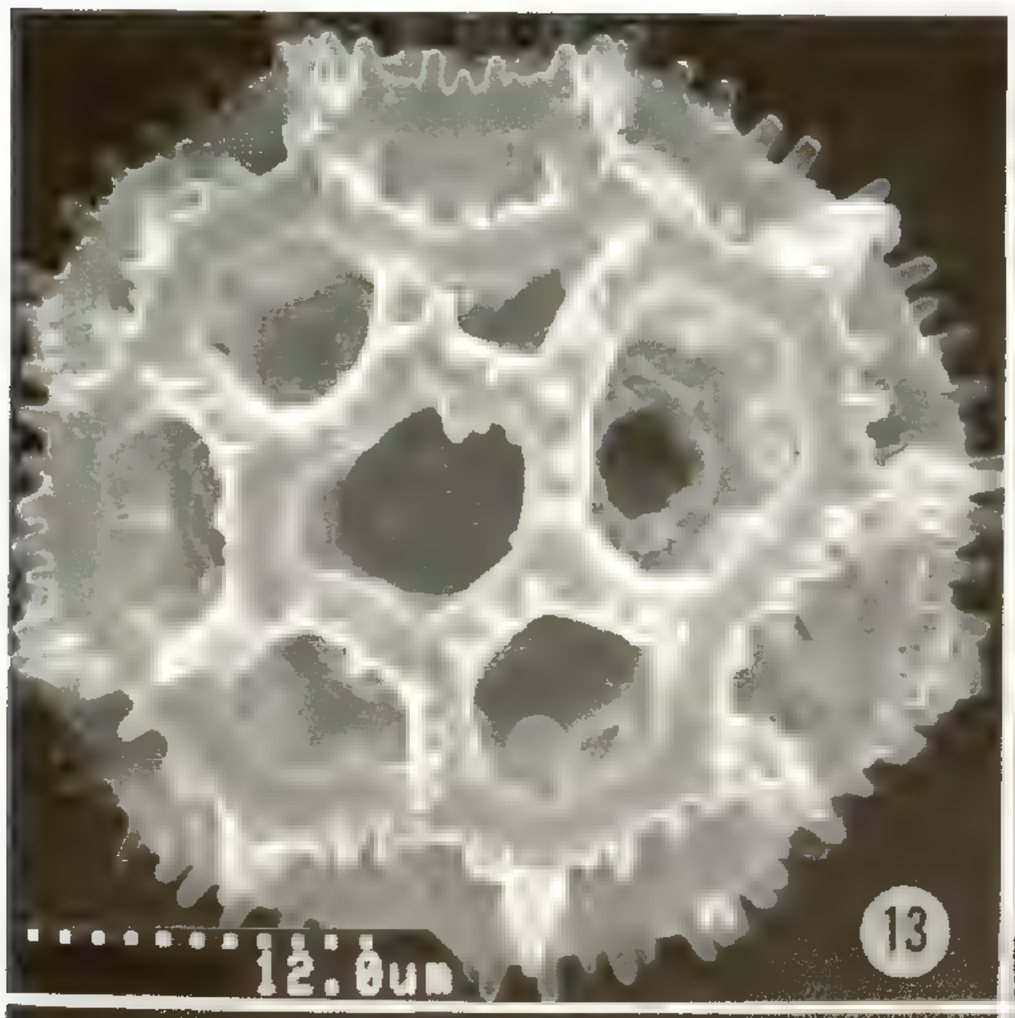
and the muri are weakly attached to the footlayer (Figures 7 and 8). Type D, which is not presently known from the Guianas, is tricolporate and lophate like Type C but without a polar areole and with cross-walls in the colpi above and below the pores. Type E, found in the Guianas in *Pacourina,* is triporate and has the complete surface covered with areoles of similar size including three that contain the pores; the muri have smooth crests without a perforated tectum, and the crests are firmly attached to the footlayer by an irregular bacular structure (Figure 18). Type F, found in *Elephantopus, Pseudelephantopus* and *Rolandra,* is triporate and multiareolate as in Type E, but usually has a perforated tectum on the muri and has many short spinules borne along the crests of the muri (Figures 10–14). Type G, found commonly in *Lepidaploa* but seen in the Guianas in *Xiphochaeta,* is tricolporate like Types C and D without the polar areoles or the divided colpi (Figure 9). Type H is added here for the pollen of the introduced *Cyanthillium,* which is areolate over the whole surface as in E and F, but has a perforated tectum on the muri, and lacks strong baculae between the intersections of the muri (Figures 15–16). Type J is added here for the unusual pollen of *Sparganophorus* that is lophate over the whole surface, triporate with short points as in F, but has low, almost sessile muri and has a weak perforated tectum continuous across the areoles (Figure 17). The low muri of *Sparganophorus* are obvious under the compound microscope, where they appear vestigial.

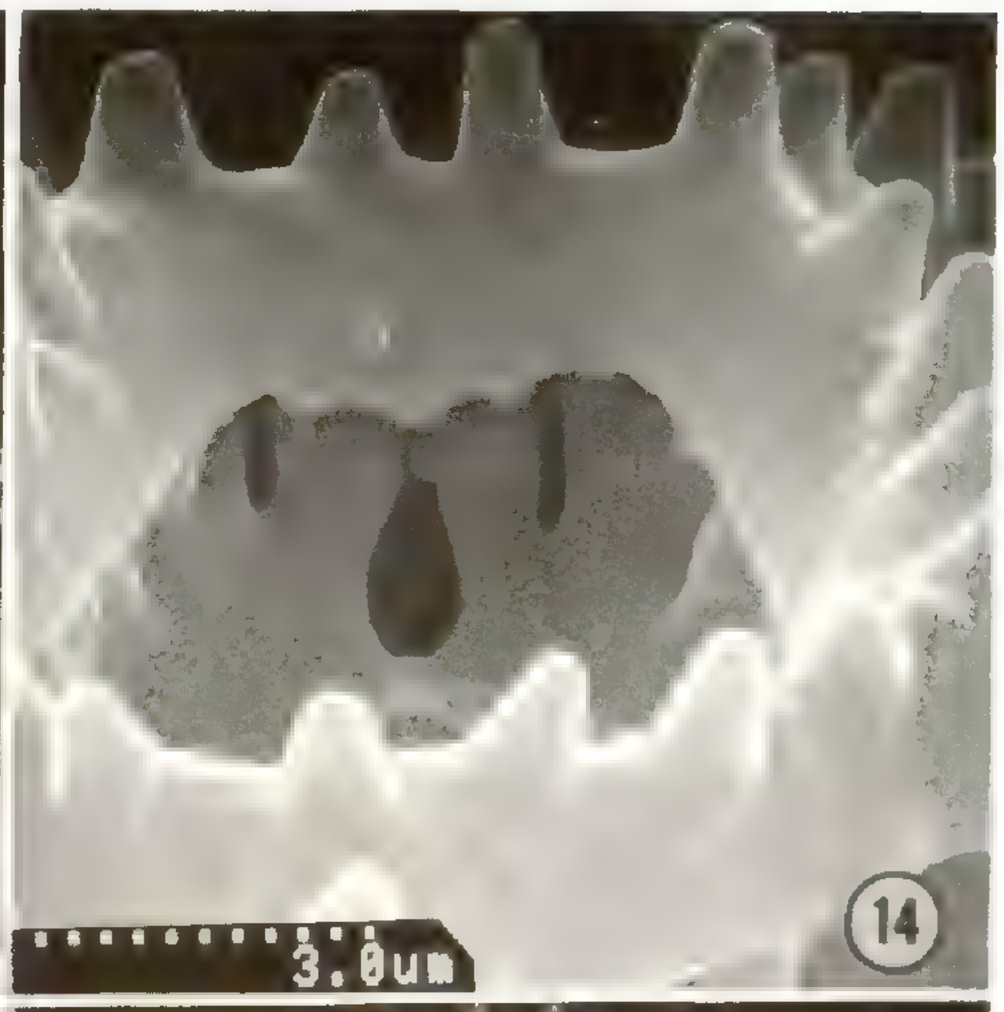
Some of the diversity of pollen in the tribe is evident in the accompanying SEM photographs for most of the genera and all the basic pollen types in the Guianas. The pollen sizes cited in the key and text are in fluid. Measurements include the tectum but exclude the projecting spine tips. Grains appear under SEM at about ⅔ of the size in fluid.

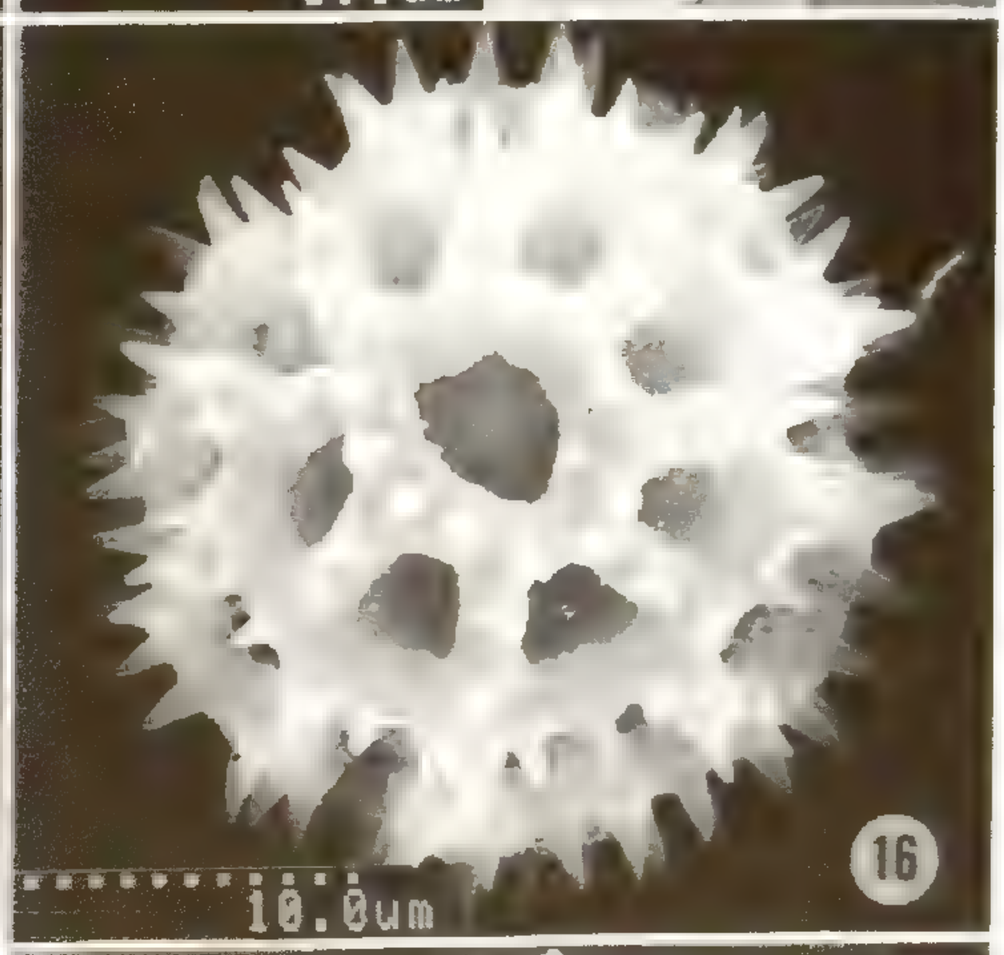
The study of the pollen suggests certain comparative relationships in the Vernoniae of the area. Among those genera included in broader traditional concepts of *Elephantopus,* both the pollen and the pappus indicate *Orthopappus* is much more distinct than *Pseudelephantopus. Orthopappus* should be maintained as distinct from *Elephantopus* even when *Pseudelephantopus* is reduced to synonymy. *Rolandra* and the closely related *Spiracantha* of Central and northern South America have the same type of lophate grains, often lacking perforations in the tectum on the muri. The generally annual nature, the distinctive foliose bracts under the

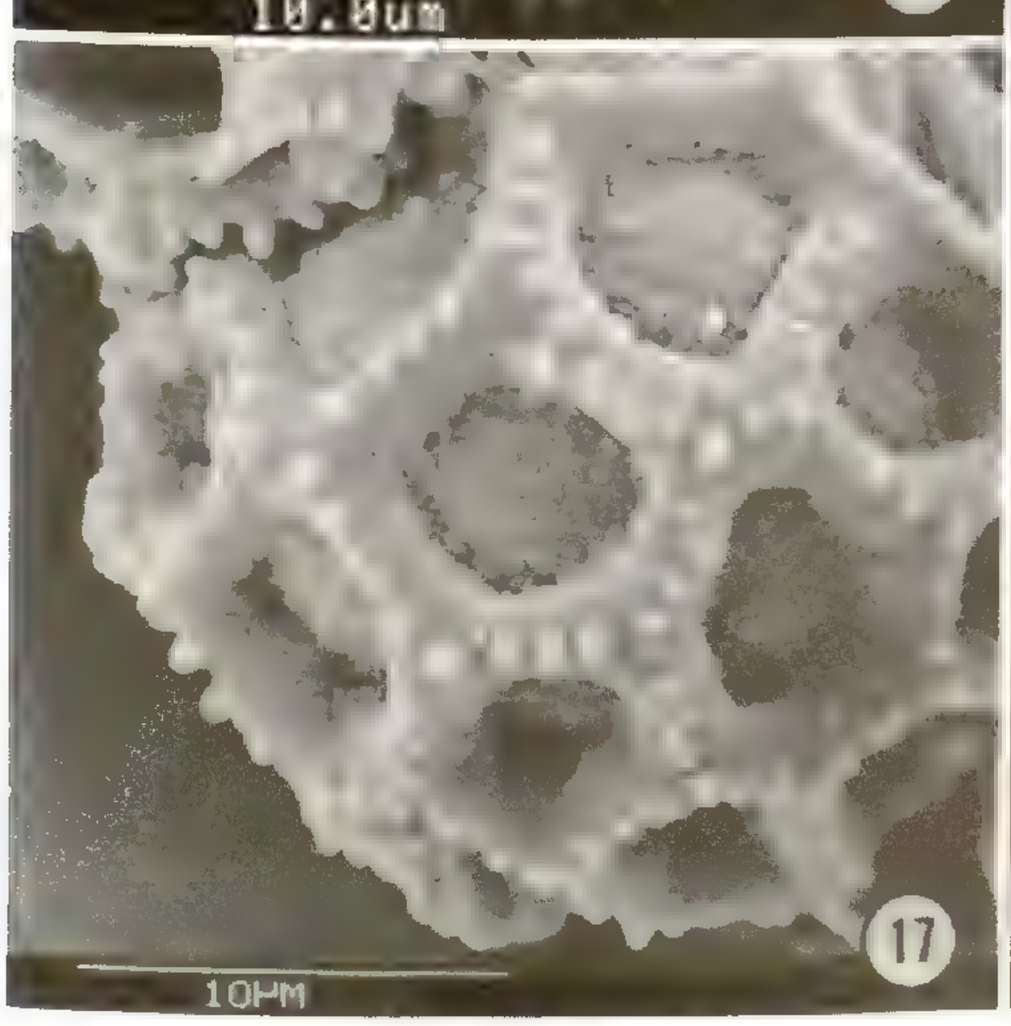


Figures 7–12. Pollens of Guiana Vernonieae, lophate forms. **7–9.** Tricolporate forms. **7, 8.** *Lepidaploa cotoneaster* (Less.) H. Robinson, Brazil, *Hatschbach 45153* (US), Type C: **7.** colpar view, **8.** polar view. **9.** *Xiphochaeta aquatica* Poeppig in Poeppig & Endlicher, Peru, *Rimachi 4672* (US), Type G, polar view. **10–12.** Triporate forms, Type F. **10, 11.** *Elephantopus mollis* H.B.K., Rota, Marianas Isl., *Fosberg 31849* (US), Type F: **10.** polar view, **11.** Detail of muri showing baculae attached to footlayer. **12.** *Pseudelephantopus spicatus* (Juss. ex Aubl.) Rohr, Cuba, *Morton 4048* (US), Type F, view showing pore.









Figures 13–18. Pollens of Guiana Vernonieae, lophate, triporate forms. **13, 14.** *Rolandra fruticosa* (L.) O. Kuntze, Brazil, *MacLeish 760* (US), Type F: **13.** view showing pore, **14.** detail of muri showing baculae attached to footlayer, variant that lacks perforations in tectum. **15, 16.** *Cyanthillium cinerea* (L.) H. Robinson, Cayenne, *Broadway 442* (US), Type H, muri near margins showing lack of baculae between junctures: **15.** view showing pore, **16.** polar view. **17.** *Sparganophorus sparganophora* (L.) Jeffrey, Venezuela, *Liesner 13370* (US), Type J, view showing low muri and showing part of adjacent broken grain. **18.** *Pacourina edulis* Aubl., Colombia, *Killip & Smith 14576* (US), Type E, view showing smooth crests of muri and irregular bacular structure.

heads of the latter, and the pappus of long scales rather than a dentate crown are the basis for its continued separate generic status.

Chromosome numbers obtained from the summary by Jones (1979) are given below in the key to the genera of the Guianas. The genera with tricolporate pollen in the Guianas show chromosome numbers mostly based on $n = 17$. The genera with triporate pollen have base numbers, where known, of $n = 8$, $n = 9$, $n = 10$, $n = 11$, or $n = 13$. Tricolporate Vernonieae with chromosome numbers near $n = 10$ are not presently known from the Guianas, and are known in the Neotropical Region only in the occasionally introduced *Baccharoides anthelminthica* (L.) Moench and *Ethulia conyzoides* L.f.

Most of the 19 species of the Vernonieae occurring in the Guianas also occur in adjacent regions such as Venezuela and Brazil. Some such as *Cyrtocymura scorpioides* occur through much of tropical America. One species, *Lepidaploa chrysotricha,* is endemic to Guyana.

ARTIFICIAL KEY TO THE GENERA OF THE VERNONIEAE IN THE GUIANAS

1. Individual heads with 1–5 (–6) florets, sometimes compacted in units of many heads 2
   2. Individual heads discrete, with many easily deciduous inner involucral bracts; pappus in 2 series; pollen Type A (as in Figures 1, 2); $n = 17$ where known 3
      3. Pappus of many bristles; anther thecae with basal tails formed with distinct sharp points of thick-walled, sterile cells; style base with broadened node and basal ring of sclerified cells; $n = 17$ . . . . . *Piptocarpha*
      3. Pappus of few flattened ribbons or short scales; anther thecae without sharp basal tails of thick-walled cells, bases blunt or with thin-walled cells; style base without node or sclerified cells . . . . . *Pollalesta*
   2. Heads compacted into secondary clusters, often grouped in axils of specialized bracts; pappus of only 1 series; $n = 8?$, $n = 11$, $n = 13$ where known 4
      4. Shrubs; clusters of heads in axils of scarcely reduced leaves, each head with 1 floret; pappus an irregularly dentate crown; achene without setulae, densely cov-

ered with glands; anther collar shorter than basal spurs of anther thecae; pollen Type F (Figures 13, 14), with or without perforations in tectum on muri, ca. 40 μm in diam.; $n = 8$? (in closely related *Spiracantha*) . . . . . *Rolandra*

4. Herbs; clusters of heads borne well above larger basal leaves, each head with usually 5 florets; pappus of bristles or awns; achene with many setulae; anther collar longer than basal spurs of anther thecae; pollen Types A or F 5
5. Pappus of many bristles; pollen a modified Type A (Figure 6), 35–40 μm in diam.; $n = 11$ . . . . . *Orthopappus*
5. Pappus of 5 awns; pollen Type F, lophate without distinct colpi (Figures 10–12), ca. 40 μm in diam. 6
6. Pappus awns highly contorted or sinuous; $n = 13$ . . . . . *Pseudelephantopus*
6. Pappus awns straight; $n = 11$ . . . . *Elephantopus*

1. Individual heads with 10 or more florets, not compacted into distinct secondary clusters 7
7. Inflorescence with heads in axils of subopposite leaves; florets of heads intermixed with narrow pales; achenes compressed, with 2 awns; pollen Type A (Figure 5), 25–30 μm in diam. . . . . *Trichospira*
7. Inflorescence with leaves or bracts alternate like the vegetative leaves; heads without pales; achenes terete or prismatic 8
8. Pappus consisting of an expanded sclerified or carnose collar, without bristles or awns; pollen Type J (Figure 17), lophate with low muri, polyhedral without colpi. weak perforated tectum in areoles, 25–35 μm in diam. . . . . *Sparganophorus*
8. Pappus without expanded sclerified or carnose collar, with bristles or awns 9
9. Pappus of many short easily deciduous segments, less than ⅓ as long as the corolla 10
10. Heads in axils of large leaves; plants semi-aquatic; leaves with weakly spinose margins; pollen Type E (Figure 18), ca. 65 μm in diam. . . . . *Pacourina*

10. Heads terminal, with subtending series of narrow foliose bracts below involucre; plants not semi-aquatic; pollen Type A (Figures 1, 2), 40–50 μm in diam.; $n = 16$ .. *Centratherum*

9. Pappus of many bristles ⅔ as long as corolla or longer, persistent to moderately deciduous 11

11. Heads never sessile; without large bracts or leaves in inflorescence; stems pilosulous with T-shaped hairs; pollen Type H (Figures 15, 16), lophate, non-colpate, ca. 40 μm in diam.; $n = 9, 10, 18$ . . . . . *Cyanthillium*

11. Heads often sessile or appearing sessile due to lateral innovation; stems with or without T-shaped hairs; pollen colpate; $n = 17$ where known 12

12. Pollen Type A; heads not borne in axils of obvious foliose bracts; raphids of achene wall short or elongate 13

13. Heads densely borne on scorpioid cymes, often contiguous; tips of involucral bracts usually pubescent on both surfaces; corolla lobes with hairs, without obvious internal resin ducts in center of lobe; raphids of achene walls elongate; pollen ca. 40 μm in diam. (Figures 3, 4); $n = 17$ . . . . . *Cyrtocymura*

13. Heads separated in cymose but not scorpioid inflorescences; tips of involucral bracts not pubescent inside; corolla lobes without hairs, often with longitudinal resin ducts filling center of lobe; raphids of achene walls subquadrate to short-oblong; pollen ca. 40 μm in diam. $n = 17$ . . . . . *Vernonanthura*

12. Pollen Types C and G; heads usually borne in axils of small or large foliose bracts; raphids of achene wall elongate 14

14. Pappus of greatly thickened somewhat deciduous subulate bristles; plants

subaquatic; achene without distinct carpopodium; anther spurs shorter than anther collar; anther appendages small, bearing glands; corolla lobes with only glands; pollen Type G (Figure 9), 37–40 μm in diam. . . . . *Xiphochaeta*

14. Pappus of slender bristles, usually with distinct outer series of persistent scales; plants terrestrial, sometimes riverine; achene with large carpopodium; spurs of anther longer than anther collar; anther appendages usually without glands; corolla lobes usually with hairs or spicules; pollen Types C (Figures 7, 8), D, G, 45–50 (–60) μm in diam.; $n = 17$ . . . . . *Lepidaploa*

Genus and Species List

COMPOSITAE: TRIBE VERNONIEAE

Centratherum Cass.
C. punctatum Cass.

Cyanthillium Blume
C. cinereum (L.) H. Robinson
[Introduced, naturalized, originally paleotropical.]

Cyrtocymura H. Robinson
C. scorpioides (Lam.) H. Robinson

Elephantopus L.
E. mollis H.B.K.

Lepidaploa (Cass.) Cass.
L. bolivarensis (Badillo) H. Robinson
(syn. *Vernonia glandulosa* Badillo, 1946, not *V. glandulosa* DC., 1836).
L. chrysotricha (Alexander) H. Robinson
L. ehretifolia (Benth.) H. Robinson
V. schomburgkiana Schultz Bip.
L. gracilis (H.B.K.) H. Robinson
V. moritziana Schultz Bip.
L. remotiflora (L. C. Rich.) H. Robinson

Orthopappus Gleason
O. angustifolius (Swartz) Gleason

Pacourina Aubl.
P. edulis Aubl.

Piptocarpha R. Brown
P. triflora (Aubl.) Benn. ex Baker

Pollalesta H.B.K.
P. schomburgkii (Schultz Bip.) Aristeg.

Pseudelephantopus Rohr
P. spicatus Rohr

Rolandra Rottb.
R. fruticosa (L.) O. Kuntze

Sparganophorus Boehm. in Ludwig.
Sparganophorus sparganophora (L.) C. Jeffrey
(syn. *Sparganophorus vaillantii* Cranz, *Struchium sparganophora* (L.) O. Kuntze).
[For discussion of the use of these names see Jeffrey (1988).]

Trichospira H.B.K.
T. verticillata (L.) Blake
(syn. *Bidens verticillata* L., *Trichospira menthoides* H.B.K.).

Vernonanthura H. Robinson
V. brasiliana (L.) H. Robinson

Xiphochaeta Poeppig in Poeppig & Endlicher
Poeppig in Poeppig & Endlicher, Nova. Gen. Sp. 3: 44. 8–11. 1843.

The genus *Xiphochaeta* is here resurrected from the synonymy of *Stilpnopappus*. The following detailed description is provided to allow proper comparison with related genera.

Plants herbaceous, aquatic or semi-aquatic annals or short-lived perennials, suberect from decumbent bases, moderately branched; stems with appressed antrorse puberulence. Leaves alternate, sessile or shortly petiolate; blades oblong to lanceolate, 2–5 cm long, 1–2 cm wide, base and apex acute, margins entire or minutely and remotely denticulate, upper surface appressed-puberulous, below glandular-punctate and minutely sparsely seriaceous, venation ascending-pinnate. Heads in axils of leaves, sessile, solitary or rarely paired or ternate, homogamous; involucral bracts 70–80, graduated, unequal, 3–4-seriate, papery, 2–4 mm long, ca. 1 mm wide, green, margins ciliate above, outside slightly pilose and glanduliferous, apex shortly aristate, spreading with age; receptacle glabrous, non-paleaceous. Florets ca. 30 in a head; corollas regular, to 3 mm long, mostly glabrous; basal tube slender, elongate; throat short, lobes bearing glands at tip; anther collar elongate, with no subquadrate cells; anther thecae small, with basal spurs shorter than the collar; style base with node; style

branches glanduliferous outside. Achenes narrowly oblong or narrowed to base, to 2 mm long, base with numerous glands, with short setulae having paired cells very unequal, rarely uniseriate, resinous idioblasts sparse, usually solitary, raphids elongate; carpopodium undifferentiated; pappus setae irregularly biseriate, rigidly subulate, incrassate, moderately deciduous, convex outside, concave inside, non-costate; outer setae ca. 15, 1.0–1.2 mm long; interior setae ca. 10, to 2.2 mm long, with ciliate margins. Pollen grains Type G, 37–40 μm in diameter (Figure 9).

The species on which the genus is based has been recognized by all authors as not being *Vernonia* because of the unusual incrassate pappus segments. These details of the pappus, along with pollen and other characters, have now shown that the species is also out of place in *Stilpnopappus,* where it was placed by Baker (1873) and other more recent authors. The name *Xiphochaeta* appropriately reflects the distinctive sword-like elements of the pappus.

The genus resembles in habit the widespread *Sparganophorus* Boehm. of both hemispheres. The latter genus has a different kind of distinctive pappus that is a sclerified collar without bristles, and the pollen is lophate of a unique form (Figure 17). Structure and geography indicate that the relationship of *Xiphochaeta* to *Sparganophorus* is rather remote.

The broadened subulate pappus segments of *Xiphochaeta* were the basis of inclusion of the species in *Stilpnopappus* Mart. ex DC. The latter genus occurs mostly in eastern Brazil with two species in Venezuela, and it has broadened, flat pappus segments with a central costa and lateral wings. *Xiphochaeta* differs clearly by the heads being in the axils of full-sized leaves, by the presence of thicker, externally convex, non-costate segments of the pappus, and by the thin-walled glanduliferous anther appendages. The anther appendages in *Stilpnopappus* are much larger, without glands, and with ornate thickenings on the cell walls, particularly in a median stripe. Pollen grains of *Stilpnopappus* are Types D and G, and are ca. 50–55 μm in diameter, much larger than in *Xiphochaeta.* The anther thecae of *Stilpnopappus* have well-developed, broad-based, and sometimes partially sterile spurs, unlike *Xiphochaeta.* The anther bases and appendages, more than any other characters, seem to negate any close relationship between *Xiphochaeta* and *Stilpnopappus.*

The closest relationship of *Xiphochaeta* is evidently to the common neotropical genus *Lepidaploa.* The habit of axillary heads,

shape of the involucre, and Type G pollen are all common in the latter genus. Pollen grains of *Lepidaploa* are mostly 45–50 μm in diameter, only slightly larger on the average than those of *Xiphochaeta*. The elongate raphids in the wall of the achenes of *Xiphochaeta* are like those seen in the present study in *Lepidaploa* and its more specialized relatives, *Chrysolaena* H. Robinson, *Cyrtocymura* H. Robinson, *Echinocoryne* H. Robinson, *Eirmocephala* H. Robinson, and *Mattfeldanthus* H. Robinson & King. These raphids differ from the short form seen in two other *Lepidaploa* relatives, *Aynia* H. Robinson and *Lessingianthus* H. Robinson, and most other neotropical Vernonieae. No raphids have been observed in one other *Lepidaploa* relative, *Stenocephalum* Schultz-Bip.

Xiphochaeta is kept separate from *Lepidaploa,* which it most closely resembles, by the thickened pappus segments, by the short spurs on the anther thecae that are much shorter than the collars, and by the total lack of a sclerified carpopodium. The carpopodium of *Lepidaploa* is usually a well-developed turbinate structure covered with sclerified cells. The anther appendage of *Lepidaploa* is larger than that of *Xiphochaeta,* and usually lacks glands, but glands have now been seen in some plants of two species, a specimen determined as *L. helophila* (Mart. ex DC.) H. Robinson from Brazil and many Central American specimens of *L. canescens* (H.B.K.) H. Robinson.

Two of the distinctive features of *Xiphochaeta* involve reduction of parts, the unsclerified carpopodium, and the reduced size of the anther thecae. Similar reduction of anther thecae, with collars longer than the spurs, is seen in members of the Vernonian subtribe Elephantopinae, which are not closely related.

The genus contains a single known species occurring in the Guianas, the Orinoco basin, and the northern Amazon basin.

Xiphochaeta aquatica Poeppig in Poeppig & Endlicher

syn. *Stilpnopappus viridis* Benth. ex Baker

Stilpnopappus aquaticus (Poepp. & Endl.) Dillon, Fieldiana, Bot. n.s. 11: 4. 1982.

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DEPARTMENT OF BOTANY
NHB - 166
SMITHSONIAN INSTITUTION
WASHINGTON, DC 20560

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CHROMOSOMES OF MEXICAN *SEDUM* VI. SECTION SEDASTRUM

CHARLES H. UHL

ABSTRACT

The four species of Section Sedastrum appear to comprise a natural group, but studies of 92 collections show three different basic chromosome numbers: $n = 20$ in *Sedum ebracteatum* and *S. hemsleyanum*, $n = 25$ in *S. hintonii*, and $n = 31$ in *S. glabrum*. The first two species are very similar and possibly should be treated as the same. Most plants of these two species are polyploids, up to $n =$ ca. 140. Many of the high polyploids are irregular at meiosis and probably reduced in sexual fertility. No clues are evident that suggest how these different basic numbers evolved.

Key Words: Crassulaceae, *Sedum*, chromosome numbers, Mexico

INTRODUCTION

This paper completes the reports on the chromosomes of the 100 or so species of *Sedum* that are native to Mexico and adjacent areas of the United States and Central America. Earlier papers (Uhl, 1976, 1978, 1980, 1983, and 1985) reported the chromosomes of 94 species and three probable hybrids that have been named as species. Methods and acknowledgements were given in Uhl (1976). Voucher specimens are in the Bailey Hortorium of Cornell University.

Rose (1905) described *Sedastrum* as a genus with clusters of dense, sessile rosettes of thick leaves and thick rootstocks. The inflorescence is an erect panicle about 30 cm high, bearing whitish flowers and dying to the base after flowering. The carpels have a distinctive basal concavity above the nectar scale. In some populations leaves and stems are streaked with red or purple, as in *Sedastrum rubricaule* Rose. More recent practice (e.g., Berger, 1930; Clausen, 1943, 1981) reduced the group to a section or subgenus of *Sedum*.

Rose (1905) recognized seven species that are distinguished from each other primarily by small differences in the shape and hairiness of the leaves. Generally following Clausen (1959, 1981), the eleven binomials that have been proposed for the species of Section Sedastrum are here reduced to four, and two of these intergrade substantially and perhaps should be combined. Three

basic chromosome numbers are found, different in each of the three more easily separated groups.

The appendix lists the species alphabetically, and the collections are listed roughly from north to south, then from east to west.

SPECIES

Sedum ebracteatum DC

Sedum ebracteatum was the first species of Section Sedastrum to be described. DeCandolle (1828) based his description entirely on a drawing by Mocino, without ever having seen a plant, living or pressed, and he did not know the locality of its origin in Mexico. Clausen (1959) reduced five species, *S. barrancae* M. E. Jones, *S. chapalense* S. Watson, *S. cordifolium* Sesse and Mocino, *S. incertum* Hemsley and *Sedastrum rubricaule* Rose, to synonymy under *S. ebracteatum,* and later (Clausen, 1981) he added *Sedastrum pachucense* C. H. Thompson here—earlier he had placed it under *S. hemsleyanum.*

Leaves of *Sedum ebracteatum* are generally puberulent, but some plants resemble *S. glabrum* in the absence of hairs. However, the two differ significantly in their chromosomes, with basic numbers of 20 in *S. ebracteatum* and 31 in *S. glabrum,* and it seems best to keep them separate. Several more or less glabrous plants from within the range of *S. ebracteatum* that were once tentatively identified as *S. glabrum* had chromosome numbers based on 20 and were reassigned to *S. ebracteatum* for that reason.

Both *Sedum ebracteatum* and *S. hemsleyanum,* are relatively common, widely distributed and a bit variable in their morphology, and some collections are more or less intermediate between them. Clausen (1959) distinguished them chiefly by the broader leaves on the floriferous branches of *S. ebracteatum,* but this character is not completely consistent. Also, leaves and stems of *S. ebracteatum* are generally a bit less hairy than those of *S. hemsleyanum,* and it has a more northerly distribution, ranging from southern Tamaulipas, Coahuila and Durango south to the trans-Mexican volcanic belt. *S. hemsleyanum* extends from the volcanic belt southeastward into Central America, with possibly some overlap in distribution.

Most collections of both *Sedum ebracteatum* and *S. hemsleyanum* are polyploid, but 20 is clearly the basic number in both,

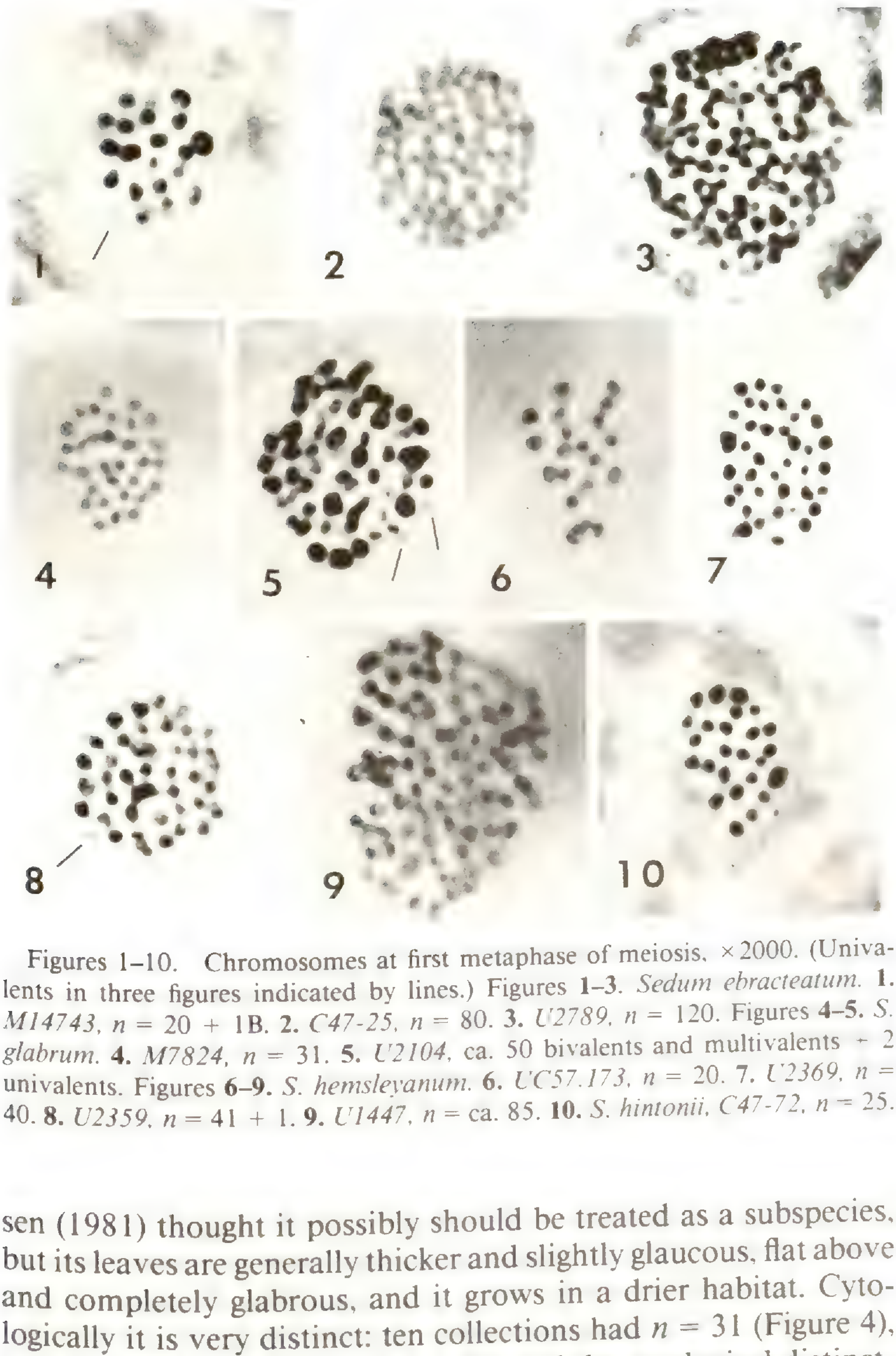
and in this regard they differ from the other two species of the section. They are treated separately here, but the difficulty in assigning some plants definitely to one species or the other and the similarity in their basic chromosome numbers make a strong case for combining them.

A plant of *Sedum ebracteatum* from Hidalgo and another from cultivation both had $n = 20$ plus a small extra chromosome that commonly was unpaired (Figure 1), but eleven other collections originating from Durango (2), Jalisco (3), Guanajuato (2), San Luis Potosi (2), Queretaro (1), and Hidalgo (1) had $n = 40$ or minor variations from that. Three more had $n =$ ca. 80 (Figure 2), 14 others had $n =$ ca. 100, four more $n =$ ca. 120 (Figure 3), and the one from farthest north had $n =$ ca. 140. Most of the higher polyploids came from more easterly localities, in the Sierra Nevada Oriental, and those with $n = 40$ came from farther west. Nearly all of the higher polyploids were very irregular at meiosis, with univalents and multivalents at metaphase I and laggards and sometimes chromosome bridges at anaphase I. These irregularities also made exact counts of many of them not possible from meiosis, and chromosome numbers given for some of them are only approximations. Several may depart substantially from exact multiples of 20.

Meiotic irregularities of this sort generally lead to unbalanced dosages of chromosomes and genes in the reproductive cells and among the progeny. In diploids this imbalance commonly reduces fertility and survival, but high polyploids by definition have more copies of each gene, and unbalanced genotypes probably are less harmful to them than they are to diploids. Nevertheless, immediately after meiosis many microspore quartets in some polyploids have spores that differ in size, and later many of the immature pollen grains are undersized. These abnormalities indicate reduced fertility, but unfortunately little information is available regarding seed production and fertility in these collections, diploid or polyploid.

Sedum glabrum (Rose) Praeger

Sedum glabrum occurs on rocks on the dry western side of the northern Sierra Madre Oriental and on the adjacent plateau in the states of Coahuila, San Luis Potosi and western Nuevo Leon of northeastern Mexico. It is similar to *S. ebracteatum,* and Clau-



Figures 1–10. Chromosomes at first metaphase of meiosis, ×2000. (Univalents in three figures indicated by lines.) Figures **1–3**. *Sedum ebracteatum*. **1.** *M14743*, $n = 20 + 1B$. **2.** *C47-25*, $n = 80$. **3.** *U2789*, $n = 120$. Figures **4–5.** *S. glabrum*. **4.** *M7824*, $n = 31$. **5.** *U2104*, ca. 50 bivalents and multivalents + 2 univalents. Figures **6–9.** *S. hemsleyanum*. **6.** *UC57.173*, $n = 20$. **7.** *U2369*, $n = 40$. **8.** *U2359*, $n = 41 + 1$. **9.** *U1447*, $n =$ ca. 85. **10.** *S. hintonii*, *C47-72*, $n = 25$.

sen (1981) thought it possibly should be treated as a subspecies, but its leaves are generally thicker and slightly glaucous, flat above and completely glabrous, and it grows in a drier habitat. Cytologically it is very distinct: ten collections had $n = 31$ (Figure 4), and one was tetraploid with $n = 62$, and the cytological distinctness argues for maintaining it as a separate species.

One collection (*U2104*) listed here appears to be a hybrid with *Sedum ebracteatum*. It formed about 50 elements at metaphase I, including about 8–10 large, multilobed multivalents and several

small univalents (Figure 5), and it had as many as five chromosome bridges at anaphase I.

Sedum hemsleyanum Rose

Sedum hemsleyanum, including *Sedastrum painteri* Rose (Clausen, 1959), has the most southerly distribution. It occurs mostly in the Sierra Madre del Sur and other southern mountains and more sparingly farther north into the trans-Mexican volcanic belt, where its distribution may slightly overlap that of *S. ebracteatum* (Clausen, 1959). A collection from Guatemala and another from Honduras both had larger leaves on the floral stems than the other collections, and both had $n = 20$ (Figure 6). However, 32 collections, mostly from the states of Puebla and Oaxaca, had $n = 40$ (Figure 7) or minor variations from that ($n = 41 + 1$ in Figure 8), and the species is primarily tetraploid. One collection from Oaxaca had $n = 60$, two from eastern Guerrero had $n =$ ca. 85 to 90 (Figure 9), one from Valle de Bravo, in the state of Mexico, had $n =$ ca. 97, another from Guerrero had $n =$ ca. 114 and one of unknown origin in the wild had $n =$ ca. 120. Most of the higher polyploids came from northerly localities for the species and possibly might more appropriately be assigned to the very similar *S. ebracteatum,* where high polyploids are common.

Sedum hintonii Clausen

Sedum hintonii is best distinguished by the dense covering of white hairs on all its stems, leaves and sepals. Described from a collection from western Michoacan, it is now known also from Jalisco and Durango (Clausen, 1981), but the three collections studied are all of unknown origin in the wild. All three have $n = 25$ (Figure 10), and this species also is distinctive cytologically.

DISCUSSION

Morphologically the four species of Section Sedastrum appear to form a natural group, more similar to each other than any of them is to any other species. However, the three basic chromosome numbers, 20, 25, and 31, present a problem in understanding relationships. Many collections of *Sedum ebracteatum* and *S. hemsleyanum* from a broad geographic range do not have exact

multiples of their apparent basic chromosome number of 20, but their cytological irregularities offer no real clues as to how the other basic numbers are related.

The significance of the meiotic irregularities that are so common in the high polyploids, especially in *Sedum ebracteatum,* also is unknown. Are the plants hybrids or apomicts, for example? Or is the meiotic irregularity tolerated because their high polyploidy buffers them against the consequences of unbalanced genotypes that would kill or sterilize a diploid? Information is needed regarding the sexual fertility of these plants in the wild.

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CORNELL UNIVERSITY
ITHACA, NY 14853-5908

APPENDIX

Chromosome Numbers

Sedum ebracteatum DC

U2052 Durango. Near Tovar, 10 km W of Tepehuanes, ca. 2000 m. *M. Kimnach & F. K. Brandt 1192.* $n = 40$.

U2581 Durango. El Salto. *A. Lau 077.* $n = 40$.

C50-16 Tamaulipas. Canyon SW of Ciudad Victoria. J. L. Edwards. $n = 140–150$.

M6321 San Luis Potosi. Limestone cliff 2.4 km E of Santo Domingo, 1540 m. R. Moran. $n = 125 \pm 10$.

U2788 San Luis Potosi. 1.5 km SE of La Salitrera, 1970 m. *R. T. Clausen 77-41.* $n = 40$.

APPENDIX
Continued

M13367 San Luis Potosi. Bluff along Rio Santa Maria at E edge of Ocampo. R. Moran & C. H. Uhl. $n = 40 + 2$.
UC50.1060 Jalisco. Barranca near Atoyac, N of Guadalajara. Lefebure. $n = 40$ prob.
U2793 Jalisco. S slope, Barranca Oblatos, N of Guadalajara, 1500 m. *R. T. Clausen 77-24*. $n =$ ca. 40.
UC53.1156 Jalisco. Near Experiencia. *J. B. Zabaleta 17*. $n = 40 + 1$.
U2115 Guanajuato. Picachos de la Bufa, NE of Guanajuato city, 2350 m. $n = 40$.
M10194 Guanajuato. Km 32, near San Juan. R. Moran. $n =$ ca. 40.
C47-49 Guanajuato. Between Dolores Hidalgo and Guanajuato city. E. J. Alexander & C. L. Gilly. $n = 100$ prob.
M14766 Guanajuato. 16 km E of San Luis de la Paz. R. Moran. $n = 90$–100.
U1844 Guanajuato. 15.7 km E of San Jose Iturbide. $n = 90 \pm 10$.
U1859 Queretaro. 11 km W of Jalpan, 1070 m. $n =$ ca. 100.
U1851 Queretaro. 1.6 km N of Camargo. $n = 115$–120.
U1487 Queretaro. Cuesta China, 3 km E of Queretaro city, 1900 m. $n =$ ca. 100.
M7673 Queretaro. Nearby locality. R. Moran. $n =$ ca. 100.
M9888 Queretaro. Nearby locality. E. Gay. $n =$ ca. 120.
U2119 Queretaro. 12 km N of Cadereyta, 2200 m. $n = 40$.
U2789 Queretaro. Gorge of San Juan River, 2.5 km S of San Juan del Rio, 1940 m. *R. T. Clausen 80-27*. $n = 120$ (Figure 3).
U1874 Hidalgo. Mex. 85, 16 km NE of Zimapan. $n = 100 \pm 2$.
M14743 Hidalgo. N of Tecozautla, 1650 m. R. Moran. $n = 20 + 1B$ (Figure 1).
M14749 Hidalgo Geysers, Tecozautla, 1550 m. R. Moran. $n = 40$.
U1542 Hidalgo. 1.6 km E of Chilcuautla. $n = 80$.
M6415 Hidalgo. Canon Venados. G. Lindsay. $n =$ ca. 100.
M7790 Hidalgo. El Carmen. R. Moran. $n =$ ca. 100.
U1472 Hidalgo. Topotype of *Sedastrum pachucense* Thompson. Hwy. 105, 0.5 km NE of Pachuca city limits. $n =$ ca. 100.
U1547 Hidalgo. 2.4 km S of Epazoyucan. $n = 100 \pm 10$.
U1411 Michoacan. Puente Rio Turundeo, 8.4 km N of Tuxpan on Mex. 15, 1830 m. $n = 118 \pm 3$.
U1442 Guerrero. Zopilote Canyon, 18.5 km N of Chilpancingo. $n = 105$-110.
C47-34 Cultivated. F. Schmoll. $n = 20 + 1$.
C47-29 Cultivated. F. Schmoll. $n = 40 + 1$.
C47-25 (Figure 2), *C47-28* Both cultivated, F. Schmoll. $n = 80 \pm 1$.
C43-25 Cultivated. R. T. Clausen. $n = 105 \pm 2$.
C47-84 Cultivated. *E. K Balls 4949*. $n =$ ca. 100.

Sedum glabrum (Rose) Praeger
U2769 Coahuila. Ridge N of San Miguel, 22 km NW of Saltillo, 1300 m. *R. T. Clausen 80-7*. $n = 31$.

APPENDIX
Continued

U1521B Coahuila. Ridge W of Mex. 57, 18 km N of Saltillo. $n = 31$.
M7824 Coahuila. Chorro Canyon, ESE of Saltillo. R. Moran. $n = 31$ (Figure 4).
U2403 Nuevo Leon. Top of cable lift, Grutas de Garcia. J. Bauml. $n = 31$.
U2402 Nuevo Leon. Huasteca Canyon. M. Flores. $n = 31$.
U1493 San Luis Potosi. Hill W of Mex. 57, 8.5 km S of Nunez. $n = 62$.
U2104 San Luis Potosi. Rocks E of Mex. 57, 1 km S of San Lorenzo. (Probable hybrid with *S. ebracteatum*.) Ca. 50 elements (Figure 5).
U2730 San Luis Potosi. 1 km S of La Zapatilla. *R. T. Clausen 80-26*. $n = 31$.
U1492 San Luis Potosi. Bluff E of Mex. 57, 1.1 km S of bridge over Rio Santa Maria. $n = 31$.
UC49.1978 Cultivated. *James West 743*. $n = 31$.
M3280, UC52.1768 Both cultivated. $n = 31$.

Sedum hemsleyanum Rose

U1424 Edo. Mexico. W side of lake at Valle de Bravo, 1800 m. $n =$ ca. 97.
C47-47, C47-48 Edo. Mexico. Barranca de Texolotengo, 6 km S of Villa Guerrero. *Gilly, Alexander* & *Xolocotzi 126* & *133*. Both $n = 40$.
U1428 Edo. Mexico. N side, Puente de Calderon, Mex 55, 12.2 km S of Villa Guerrero. $n = 40$.
U1464 Morelos. Probable topotype of *Sedastrum painteri* Rose. El Salto de San Anton, W of Cuernavaca. N. W. Uhl. $n = 40$.
U1290 Morelos. 9 km from Cuernavaca on road to Tepoztlan. *M. Kimnach K374*. $n = 40$.
U2355 Puebla. 4.3 km E of Aquixtla, 2050 m. $n = 41$.
U1449 Puebla. Canyon 1.5 km E of Tepenco. $n = 40$.
U1450 Puebla. 2.4 km SE of El Tepenene. $n = 40$.
U1451 Puebla. Bluff 17.3 km SW of Acatlan, 1300 m. $n = 40$.
U1655 Puebla. Nearby locality. *W. Handlos 407A*. $n = 40$.
M6399 Puebla. River cliffs near Petlalcingo, 1325 m. R. Moran. $n = 40$.
U2359 Puebla. 6.4 km N of Penafiel. $n = 41 + 1$ (Figure 8).
M6359 Puebla. San Antonio Texcala, near Tehuacan. R. Moran. $n = 39 + 1$.
M6360 Puebla. Nearby locality. R. Moran. $n = 40$.
OM4 Veracruz. W of Maltrata. R. T. Clausen. $n = 40 + 2$.
U1888 Veracruz. S side of Rio Blanco, opposite city. $n = 40$.
O-RB2 Veracruz. Nearby locality. R. T. Clausen. $n = 39$–40.
C47-102 Guerrero. 25 km W of Iguala on road to Teloloapan. L. F. Randolph. $n = 114 \pm 2$.
U1447 Guerrero. 11 km NE of Taxco. $n = 85 \pm 3$ (Figure 9).
M10169 Guerrero. Canon del Mano, near Iguala. R. Moran $n = 40$.
U1440 Guerrero. 8.5 km E of Chilpancingo. $n =$ ca. 90.
M6366 Oaxaca. 6 km N of Miltepec, 2050 m. R. Moran. $n = 40$.
U1453 Oaxaca. 2.5 km S of Camotlan. $n = 40$.
U2866 Oaxaca. 14 km NE of Teotitlan del Camino. 1525 m. $n = 40$.
U2658 Oaxaca. Nearby locality. *J. Bauml* & *M. Kimnach 392*. $n = 40$.
U2411 Oaxaca. 11 km NW of Yanhuitlan. $n = 40$.

APPENDIX
Continued

U2092 Oaxaca. Nearby locality. *W. Handlos 542A.* $n = 40$.
U2095 Oaxaca. Ca. 19 km NE of Yolomecatl. *W. Handlos 552B.* $n = 40$.
U2319 Oaxaca. Near Tlaxiaco, 1980 m. *F. Boutin 3941.* $n = 40 + 1$.
U2306 Oaxaca. Ixtlan. T. MacDougall. $n = 40$.
M7777 Oaxaca. San Hipolito. R. Moran. $n = 40$.
C47-50 Oaxaca. Sierra de San Felipe. A. J. Sharp. $n = 40$.
U2369 Oaxaca. Ca. 5 km E of Oaxaca city, 1800 m. $n = 40$ (Figure 7).
U1650 Oaxaca. 18 km of Totolapan. *W. Handlos 331A.* $n = 40$.
U1353 Oaxaca. Rio de Lapaguia, Miahuatlan. *T. MacDougall B-251.* $n = 60$.
UC57.246 Guatemala: Dept. Sacatepequez. Epiphytic near Alotenango, 1350 m. C. K. Horich. $n = 20$.
UC57.173 Honduras: Dept. Francisco Morazan. E slope of Cerro Berrinche. C. K. Horich. $n = 20$ (Figure 6).
C-47-3 Cultivated. Schmoll. $n = 120 \pm 2$.
C47-87 Cultivated. T. MacDougall. $n = 40$.

Sedum hintonii Clausen

U1746 Cultivated. J. Marnier-Lapostolle. $n = 25$.
U2689 Cultivated. Univ. of Guadalajara. $n = 25$.
C47-72 Cultivated. F. Schmoll. $n = 25$ (Figure 10).

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ON THE ETYMOLOGY OF *VACCINIUM* L.

S. P. VANDER KLOET

In most botanical works, the name *Vaccinium* is not translated as a rule, but in those few cases where the author appears to have given the word some thought, the usual solution has been to issue the following statement: an ancient Latin name of obscure derivation (Johnson, 1636; Smith *in* Rees, 1817; Gray, 1848; Rehder, 1927) presumably from the Latin *vaccinus,* of cows (Fernald, 1950). However, both Johnson and Smith also suggest that *Vaccinium* is possibly derived from the Greek *Hyacinthos.* This notion is still given credence in the most recent *Oxford Latin Dictionary* (Glare, 1982) where *Vaccinium* is defined as a possible corrupt form of *vakinthos,* a term for a dark-flowered plant such as an orchid or fritillary. The purpose of this paper is to present an argument against the derivation of *Vaccinium* from *vakinthos.*

The word "*Vaccinium*" is first encountered in Virgil's *Eclogues* where he uses it in the following lines: "*alba ligustra cadunt, vaccinia nigra leguntur*" (Ecloga II: 18); "*mollia luteola pingit vaccinia caltha*" (Ecloga II: 50); and "*et nigrae violae sunt et vaccinia nigra*" (Ecloga X: 39).

These quotations have been translated by Dryden (1880) as follows:

"White lilies lie neglected on the plain While dusky hyacinths for use remain" (Ecl. 2: 18)

"And set soft hyacinths with iron blue, To shade marsh marigolds of shining hue;" (Ecl. 2: 39)

"Tho' Phyllis brown, tho' black Amyntas were, Are violets not sweet, because not fair" (Ecl. 10: 39)

And in a more pedestrian manner by Fairclough (1960):

"The white privets fall, the dark hyacinths are culled" (Ecl. 2: 18)

"Sets off the delicate hyacinth with the golden marigold" (Ecl. 2: 50)

"Violets, too, are black and black are hyacinths" (Ecl. 10: 39)

Later usage by Vitruvius (7.14.2) "*Eadem ratione vaccinium temperantes et lactem miscentes purpuram faciunt elegantem*"

and by Ovid (Tr. 1.1.5) "*nec te purpureo velent vaccinia fuco*" suggest that a dark purple dye was extracted from *Vaccinium.* Pliny (Nat. 16: 77) merely mimics Virgil "*salices . . . ligustra tesseris utilissima item vaccinia Italiae*" but erroneously has both *Vaccinium* and *Salix* growing in swamps along with *Alnus* and other species of wet sites.

Since corollas from hyacinths, fritillaries, and orchids are not known for their natural dyes (McGrath, 1977) the apparent contradiction (especially between the translators of Virgil and those of Ovid and Vitruvius) is nevertheless easily resolved if the labial "B" is substituted for "V," as was first proposed by Johnson (1636: 1418) who argued that "Baccae may be called berries, *Vaccinia* as though they should be called *Baccinia.*"

The pronunciation of "B" (β in Greek) as "V" was becoming common not only in Hellenistic Greek (Browning, 1983) but it also began to occur in vulgar Latin, especially during the Principate, while at the same time "V" ceased to be pronounced as "W" (Haadsma and Nuchelmans, 1963). In short, "B" and "V" were moving towards a common pronunciation and could be confused. Virgil (70 BC–19 BC) was born and raised near Mantua in Cisalpine Gaul where he would have seen (and possibly eaten) the bilberry with its dark blue-black fruit, as well as privet (*Ligustrum*) and bindweed (now *Convolvulus,* but probably called *Ligustrum* in Virgil's time according to Page, 1960). As a linguist and poet, Virgil would have been aware of this trend where "V" was substituted for "B" and might have made use of it in his first major collection of poems. Thus, if we then also substitute *Baccinia* for *Vaccinia* in his *Eclogues,* and translate the word as "berry", the lines cited above make more sense and the result jibes with the usage of Ovid and Vitruvius.

"The white privet falls, the black berries are picked" (Ecl. II: 18). Regardless, whether *ligustra* is translated as privet or bindweed, the corollas are either short-lived or stink, or both. "He paints soft berries and mellow-yellow marsh marigolds" (Ecl. 2: 50). "Black berries and dark Violets" (Ecl. 10: 39). These simple yet pleasing images are well in line with the usage apparently envisioned by both Ovid and Vitruvius, who are both correct in their assessment of the dyeing properties of bilberries, whortleberries and blueberries. Recall the current television advertisement where the Efferdent solution quickly removes the dark blue-violet stain from a string of genuine pearls extracted from a blueberry pie.

Some purists may argue that this interpretation detracts from the elegance of the *Eclogues* and makes them more vulgar but let us remember that they are basically poems about bucolic leisure. But this interpretation resolves a dichotomy in meaning and unifies ancient usage with current usage, where *Vaccinium* is a large cosmopolitan genus of small-berried shrubs and trees. The only proviso centers on the absence of *Vaccinia* in any known classical Latin text. Nonetheless the etymology *bacca* → *Vaccinium* is the most likely, although admittedly decisive textual proof is wanting.

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BIOLOGY DEPARTMENT
ACADIA UNIVERSITY
WOLFVILLE, NOVA SCOTIA
CANADA B0P 1X0

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ECOLOGICAL ASPECTS OF *ARETHUSA BULBOSA*, *CALOPOGON TUBEROSUS* AND *POGONIA OPHIOGLOSSOIDES* (ORCHIDACEAE) IN EASTERN NEWFOUNDLAND. II. PARTITIONING OF THE MICROHABITAT

J. Todd Boland and Peter J. Scott

ABSTRACT

Three sympatric species of peatland orchids were investigated for differences in their ability to partition microhabitats. Species distributions at the study sites reflected differences in the hydrology and microtopography, indicating microhabitat partitioning. *Pogonia* was restricted to the wettest areas while *Calopogon* and *Arethusa* were found on drier sites.

Key Words: Peatland orchids, *Arethusa, Calopogon, Pogonia,* microhabitat, Newfoundland

INTRODUCTION

Peatlands are a significant vegetation type of Newfoundland, with 18 of the 32 species of Newfoundland orchids inhabiting these peatland environments. Various plants within a particular peatland may appear to be evenly distributed; however, upon closer inspection, the species is seen to have a specific distribution pattern. This pattern often reflects microhabitats within a peatland.

Differences in the growth rates of various peatland plants, especially *Sphagnum* spp. and sedges, create a hummocky terrain. These hummocks often remain above the watertable year-round, while in hollows the watertable is usually at the surface. The species within a peatland community are often distributed relative to the watertable. Thus, while cranberry (*Vaccinium macrocarpon* Ait.) and sheep laurel (*Kalmia angustifolia* L.) commonly co-occur on a particular peatland, the former species is distributed near the watertable while the latter is often confined to the drier hummocks (Wells, 1981).

Arethusa bulbosa L., *Calopogon tuberosus* (L.) BSP and *Pogonia ophioglossoides* (L.) Ker are three sympatric Newfoundland orchids which frequently grow on the peatlands of the Avalon Peninsula (Luer, 1975).

This study was undertaken to determine how these three species

are distributed when they co-occur. Do they partition the microhabitats of the peatlands they inhabit? Microhabitat partitioning is defined in this study by the species' distributions in relation to hydrology and microtopography of the peatland.

METHODS AND MATERIALS

Three study sites were located about 40 km west of St. John's, Newfoundland in the vicinity of the Witless Bay Line. Site 1: elevation 216 m; 47°22′00″N; 53°02′51″W; site 2: elevation 231 m; 47°20′35″N; 52°59′14″W; site 3: elevation 197 m; 47°20′19″N; 52°55′52″W. Two study sites were slope bogs, the most common peatland type on the Avalon Peninsula (Wells, 1981). These treeless bogs are rarely more than 2 m deep, with slopes from 5–15%. The watertable is usually at or near the surface. Underlying bedrock is mostly acidic; seepage waters are generally nutrient-poor.

The third study site was a ribbed fen, an uncommon peatland type on the Avalon Peninsula (Wells, 1981). These severely-wind-swept peatlands occur on exposed slopes, usually over 200 m in elevation. They are treeless and shallow, mostly less than 1 m in depth. Ribbed fens may contain exposed rock outcrops and glacial erratics. Flashets or small pools in ribbed fens are common and are oriented at right angles to the slope. These fens are generally more minerotrophic than slope bogs as the nutrients are released by high soil-frost activity and continual downslope water movement (Wells, 1976).

Field work was conducted from June to September, 1988. A 10 m^2 plot was delineated at each site and each plot was subdivided into 400 0.5 m^2 quadrats. *Arethusa, Calopogon* and *Pogonia* plants were counted and mapped, and elevation above the watertable was determined in each quadrat.

Microtopography of each plot was determined. Mean height above the watertable for the orchids was estimated with the surface of the nearest flashet taken to be height zero. This estimation was based on the quadrat's mean height for all quadrats containing at least one orchid species.

Two peat samples were taken from each plot. Since *Pogonia* was noted to occur separately from *Arethusa* and *Calopogon*, one sample was taken near a group of *Pogonia* and the other near a group of *Arethusa* and *Calopogon*. Cores were analyzed for nutrient content, pH and water content.

To determine if two orchid species within a site were distributed separately from one another, 0.5 m^2 quadrats that contained at least one individual were examined by a z-test (Wetherill, 1967). A z-score of 1.97 or higher was taken to indicate that the observed number of individuals of a species was significantly higher than expected for that quadrat. If over 5% of the total quadrats within a site showed significant z-scores, then the two species were taken to be significantly separate from each other.

RESULTS

Analysis of peat samples showed that the nutrient content was variable from site to site but pH and percent of available nitrogen were less variable. There was no significant relationship between the distribution of the three orchid species and availability of nutrients.

Based on z-scores, in sites 1 and 3, *Pogonia* was significantly clumped apart from *Arethusa* and *Calopogon*; *Calopogon* and *Arethusa* overlapped in their distribution. In site 2, none of the orchids was significantly separate from the others.

Mean water content of the substrate near *Pogonia* was 92.4% (range = 91.3–93.5%) at all sites. In sites 1 and 3, *Pogonia* was found to be restricted to the perimeters of flashets which had gently sloping sides (a slope of 1–2%). Site 2, however, had *Pogonia* abundant throughout, distributed from 1 to 11 cm above the watertable (mean = 4.9 cm, SD = 1.96). The frequency of quadrats containing *Pogonia* reached a maximum for those quadrats which were 5 cm above the watertable (Figure 1).

Calopogon and *Arethusa* were found close to steep-sided flashets and on the sides and tops of peat hummocks, especially at sites 1 and 3. At site 2, *Arethusa* was restricted to the few hummocks present but *Calopogon* was found in many of the depressions as well. The mean water content near these species was 78.2% (range = 75.4–80.7%).

Microtopography of site 1 had elevations ranging from 0 cm (surface of the flashets) to 36 cm above the watertable. Orchids of this site were restricted to 1 to 29 cm above the watertable. Sites 2 and 3 had elevations above the watertable ranging from 0 to 32 cm and 0 to 36 cm respectively. At site 2, orchids were restricted to 1 to 23 cm above the watertable while at site 3, they were distributed from 1 to 25 cm.

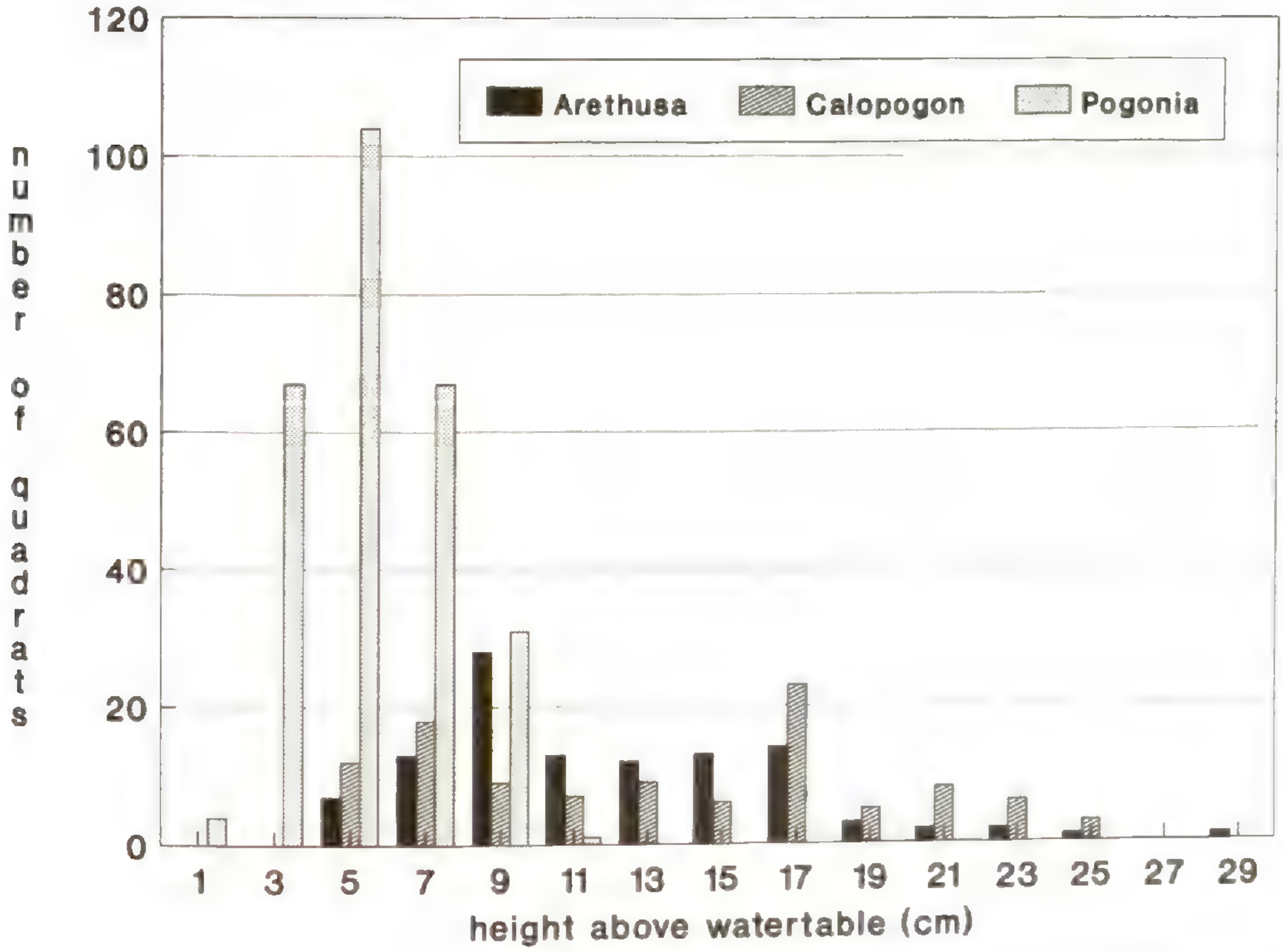

Figure 1. Frequency of quadrats containing *Arethusa, Calopogon* or *Pogonia* at various heights above the watertable.

Arethusa was found from 5 to 25 cm above the watertable (mean = 12.1 cm, SD = 4.72). The frequency of quadrats containing *Arethusa* reached a maximum for those quadrats which were 9 cm above the watertable (Figure 1).

Calopogon ranged from 5 to 29 cm above the watertable (mean = 12.9 cm, SD = 5.96). The two orchids had a bimodal distribution with the frequency of quadrats containing them peaking at 7 and 17 cm above the watertable (Figure 2).

DISCUSSION

Analysis of the nutrient content in areas of *Pogonia, Calopogon* and *Arethusa* within each site did not show any patterns. Distribution of orchids in these particular sites did not appear to be influenced by the availability of nutrients.

The distribution of *Pogonia* individuals in relation to the microtopography showed them to be mostly in the wettest areas of the three sites (mostly 3 to 9 cm above the watertable). *Calopogon* and *Arethusa* individuals were found close to steep-sided flashets

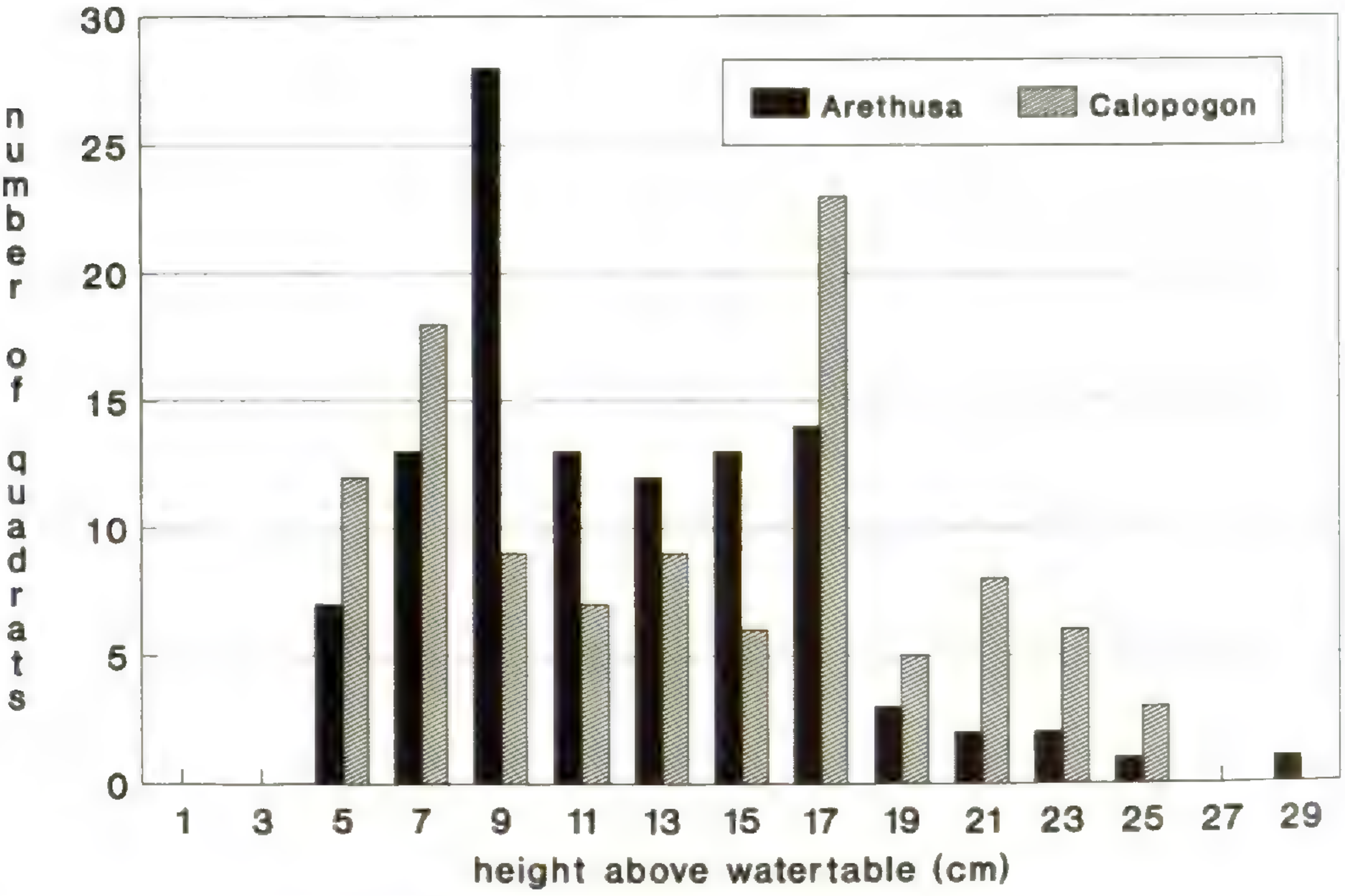

Figure 2. Frequency of quadrats containing *Arethusa* or *Calopogon* at various heights above the watertable.

but were mostly distributed in somewhat drier areas on the sides and tops of peat hummocks.

Case (1964) found all three species co-occuring in the Great Lakes region. He noted *Pogonia* as being most abundant in the wetter bogs and swamps, *Arethusa* frequently growing on sedge tufts among flashets as well as on isolated sphagnum hummocks, and *Calopogon* being common on the edge of hummocks and around the base of stunted spruce.

Petrie (1981) also noted that while these three orchids often co-occur, *Pogonia* was usually most common in the wettest part of a bog, and its orchid companions, although nearby, were mostly distributed in somewhat drier situations.

The distribution pattern of the orchids in this study can be partly explained by physical features of the orchid's root-systems. *Pogonia* individuals have a fine, fibrous root-system which grows superficially, thus *Pogonia* is not tolerant of drought conditions (Luer, 1975). Gentle shorelines of flashets and low depressions are the areas of a peatland which have the least possibility of becoming droughty. *Calopogon* and *Arethusa* have root-systems which bear small, rounded bulbous corms (Luer, 1975) which can act as water-storage organs. Thus, these orchids apparently can

tolerate the drier conditions found on the sides and tops of peat hummocks.

Statistics from this study show the distribution of *Pogonia* to be separate from *Calopogon* and *Arethusa*. The latter two orchids overlap in their distribution; mean height above the watertable for *Calopogon* and *Arethusa* was 12.9 cm and 12.1 cm, respectively. However, *Calopogon* and *Arethusa* were not evenly distributed throughout their overlapping microhabitat. Both orchids appear at 5 cm above the watertable. Below 9 cm and above 15 cm, *Calopogon* is the most abundant, while between 9 and 15 cm above the watertable, *Arethusa* is more common. While the differences in the distribution of *Calopogon* and *Arethusa* are subtle, the pattern of distribution found in this study suggests that *Calopogon* is more tolerant of wetter and drier conditions than is *Arethusa*.

Factors other than hydrology of these peatlands may be affecting distributions of *Calopogon* and *Arethusa* in particular. Further investigation is necessary to ascertain what other factors might affect the distribution of these orchids.

This study suggests that in eastern Newfoundland, hydrology is a major factor affecting partitioning of microhabitats for these three sympatric orchids. *Arethusa, Calopogon* and *Pogonia* have overlapping distributions throughout the northeastern United States and eastern Canada from the Great Lakes to Newfoundland. While hydrology may be a major factor affecting the partitioning of microhabitats for the three orchids throughout their geographic range, other factors may also affect their distribution within a given peatland.

These other factors may include the hydrology pattern of a particular peatland type. Watertable patterns may vary considerably between a ribbed fen and a basin bog (Wells, 1981). Different plant associations within a peatland site have different key species, which may prevent one or more of the orchids from becoming established. For example, Sheviak (1974) found *Pogonia* to be absent from areas where leatherleaf, *Chaemadaphne calyculata,* was present.

Throughout North America, much of the emphasis on orchid ecology is based on their pollination ecology (Thien and Marcks, 1972). Orchids which co-occur at a particular site are often studied to determine differences in their breeding systems. Few studies have been done on how the orchids co-exist, based on the ecology

of their particular site preferences. Such factors affecting the partitioning of microhabitats between sympatric orchids should be the subject of further investigations within the Orchidaceae.

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DEPARTMENT OF BIOLOGY
MEMORIAL UNIVERSITY OF NEWFOUNDLAND
ST. JOHN'S, NEWFOUNDLAND
CANADA A1B 3X9

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TWO NEW COMBINATIONS AND A NAME CHANGE FROM THE LONG EXPEDITION OF 1820

GEORGE J. GOODMAN AND CHERYL A. LAWSON

ABSTRACT

A new combination is provided for a *Scutellaria* and an *Engelmannia*. A name change in *Mimulus* is explained.

Key Words: *Scutellaria, Engelmannia, Mimulus,* Long Expedition

The Long Expedition to the Rocky Mountains in 1820 included on its scientific staff Edwin James, M.D., as botanist, geologist and surgeon. In our work on the botany of this expedition, we find it necessary to make some new combinations and a name change preparatory to our extensive publication on the expedition.

Scutellaria parvula Michx. var. **missouriensis** (Torr.) Goodm. & Laws., *comb. nov.*

#338 *S. ambigua* Nutt. *β missouriensis* Torr., Ann. Lyc. Nat. Hist. N.Y. 2: 232.1827. "Council Bluff, on the Missouri." The type was collected by James.

Torrey's description of var. *missouriensis,* an overlooked, earlier epithet, fits the current concept of *Scutellaria parvula* var. *leonardi* (Epling) Fernald, Rhodora 47: 172.1945. This latter name and its basionym *S. leonardi* Epling, Amer. J. Bot. 26: 20.1939, now become synonyms of var. *missouriensis.*

Engelmannia peristenia (Raf.) Goodm. & Laws., *comb. nov.*

Silphium peristenium Raf., Atl. Jour. 1: 146.1832. "S[ilphium] anon T[orrey].239." Based on the following:

#239 *Silphium n. sp. Nutt. mss.* in Torr., Ann. Lyc. Nat. Hist. N.Y. 2: 215.1827. The type was collected by James but cannot be located at NY. Torrey described James's plant as "A singular species, with pinnatifid leaves, and the scales of the involucrum very narrow. Mr. Nuttall found the same on the Red River."

Engelmannia pinnatifida Nutt., Trans. Am. Phil. Soc. ser. 2, 7: 343.1840. "The plains of Red River." This collection was made in Oklahoma by Nuttall in 1819.

Engelmannia pinnatifida T. & G. in Nutt., l.c. *fide* Torrey & Gray, Fl. No. Am. 2: 283.1842. "Silphium, n.sp. (Nutt.) Torr. in ann. lyc. New York, 2. p.215. On the Canadian, *Dr. James!* Red River, Arkansas, *Nuttall!*. . . ."

Although the authorship of *Engelmannia pinnatifida* has nothing to do with our new combination, it is interesting to note that in some twenty floras and manuals of this century that include this genus, about half use Torrey and Gray, several use Nuttall, some use Gray, and one uses Gray ex Nuttall.

Following Article 57.3 of the 1988 *International Code of Botanical Nomenclature* (often referred to as the Demoulin Rule), the plant *Mimulus glabratus* HBK. var. *fremontii* (Benth.) Grant should again be called *Mimulus glabratus* HBK. var. *jamesii* (T. & G.) Gray.

The autonym var. *jamesii* was established by *Mimulus jamesii* var. *fremontii* Benth. This autonym has priority over the epithet var. *fremontii.*

The pertinent synonymy is as follows:

Mimulus glabratus HBK. var. **jamesii** (T. & G.) Gray, Syn. Fl. No. Am. ed. 2, 2(1): Suppl. 447.1886.

M. jamesii T. & G. ex Benth. in DC., Prodr. 10: 371.1846. TYPE: *James* (NY). Along the Missouri River in Pottawatamie Co., Iowa, May 27, 1820.

M. jamesii T. & G. ex Benth. var. *fremontii* Benth. in DC., Prodr. 10: 371.1846. TYPE: *Fremont* (NY). Laramie Co., Wyoming, July 14, 1842.

M. glabratus HBK. var. *fremontii* (Benth.) Grant, Ann. Mo. Bot. Gard. 11: 190.1924.

DEPARTMENT OF BOTANY AND MICROBIOLOGY
UNIVERSITY OF OKLAHOMA
NORMAN, OK 73019

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ADDITIONS TO THE FLORA OF NEWFOUNDLAND. II

STUART G. HAY, ANDRE BOUCHARD, LUC BROUILLET AND MARTIN JEAN

ABSTRACT

Two significant additions have been made to the native vascular flora of Newfoundland as a result of explorations on the Great Northern Peninsula: *Cardamine bellidifolia* L. and *Salix cordata* Michx.

Key Words: Vascular plant flora, additions, Newfoundland

Our understanding of the vascular flora of Newfoundland rests largely on the work of M. L. Fernald (1911, 1926, 1933), and of E. Rouleau (1978, unpublished distribution maps and compiled herbarium records). As a result of their considerable contributions, and a long history of botanical exploration by other botanists that began with the voyage of Sir Joseph Banks in 1766, today, the flora of the island is relatively well known. Even so, parts of the island remain poorly explored, particularly the more inaccessible interior plateau regions, and exciting new discoveries will continue to be made as botanists further explore this vast territory.

Our research on the rare vascular plants of the island (Bouchard et al., 1991), and our earlier work on the flora of the west coast and Gros Morne National Park, have resulted in the addition of many new records to the native flora of the province (Hay et al., 1990). In 1991, we pursued our investigations on the rare plants and general flora in Port au Choix National Historic Park and the region of Canada Bay on the Great Northern Peninsula. Included in this report are notes on the habitat and distribution of two remarkable species that were collected for the first time on the island during these field explorations. Both species must be added to the list of rare plants of Newfoundland (Bouchard et al., 1991).

Cardamine bellidifolia L.

SPECIMENS. White Bay North Distr.: Chimney Bay, Cloud Hill, 1991/08/08, *Bouchard, Hay, Brouillet & Jean 91417* (CAN, MT).

Cardamine bellidifolia is a circumpolar, arctic-alpine plant ranging as far south in the Cordillera of western North America as northern California, whereas in the east, it lies mostly to the north of 55 latitude N (northern Québec/Labrador Peninsula, Ellesmere Is., Greenland). Rare disjunct occurrences are found southward in Maine (Mt. Katahdin, West Baldwin), New Hampshire (Mt. Washington), and in the Shickshock Mountains of Québec's Gaspé Peninsula (Crow, 1982; Scoggan, 1978–79).

At Chimney Bay, Cloud Hill is a high, barren, wind-swept mountain (alt. 1147 ft.) lying along the northern reaches of the Long Range Mountains. At several sites near the summit, *Cardamine bellidifolia* was discovered growing in moist cracks of the barren siliceous bedrock. The tiny plants were most inconspicuous and fewer than fifty individuals were observed.

The discovery of this species on the Great Northern Peninsula of Newfoundland adds yet another species to an already impressive list of wide-ranging, arctic-alpine plants that are restricted to the Long Range Mountains or to the northern tip of the Peninsula; some of these include *Lycopodium alpinum* L., *Oxyria digyna* (L.) Hill, *Ranunculus pedatifidus* J.E. Sm. ex Rees, *Salix herbacea* L., *Saxifraga rivularis* L., and *Sibbaldia procumbens* L. These arctic-alpine species have ranges extending southward in the eastern part of the continent to isolated or disjunct alpine habitats such as occur in the mountains of the Long Range of western Newfoundland, the Shickshocks of Québec, and outposts in northern New England.

Salix cordata Michx.

[syn.: *S. adenophylla* Hook., *S. syrticola* Fern.]

SPECIMENS. St. Barbe South Distr.: Pointe Riche Peninsula, pond south of Port au Choix Cove, 1991/08/01, *Bouchard, Hay, Brouillet & Jean 91106* (CAN, GH, MT).

The range of *Salix cordata* extends from southern Hudson Bay and James Bay (Ontario, Québec), southward to the lower Great Lakes (Ontario, Illinois, Michigan), with isolated occurrences eastwards in Québec, southern Labrador and northern Maine (Soper and Heimburger, 1982). Although *S. cordata* has been attributed to the flora of Newfoundland, its presence there has never been substantiated (G. Argus, pers. comm.). All previous reports, including those of Fernald, are based on misidentifica-

tions of specimens presently referred to *S. eriocephala* Michx. (*S. rigida* Muhl.; *S. cordata* Muhl., not Michx.) or *S. glaucophylloides* Fern. (*S. myricoides* Muhl.), and on misapplication of the name *S. cordata* Michx. to specimens identified as *S. cordata* Muhl., a synonym of *S. eriocephala.*

The discovery of Heart-leaved willow in Port au Choix National Historic Park is the first authentic report for the island of Newfoundland. Despite the confusion which appears to reign among herbarium specimens, *Salix cordata* is an unmistakably distinctive willow, particularly in the field, where its form and foliage are quite striking. The population, which appears to consist of a single clone of about fifty individuals, was found in an open, minerotrophic larch fen, bordering a large pond.

The Port au Choix Peninsula harbors several other rare or noteworthy species of willows that occur in different habitats on the limestone barrens, including *Salix arctophila* Cockerell, *S. ballii* Dorn, *S. lanata* L. ssp. *calcicola* (Fern. & Wieg.) Hult., *S. myrtillifolia* Anderss., *S. pedunculata* Fern., *S. reticulata* L., and *S. wiegandii* Fern.

ACKNOWLEDGMENTS

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INSTITUT DE RECHERCHE EN BIOLOGIE VEGETALE
JARDIN BOTANIQUE DE MONTREAL
4101 EST, RUE SHERBROOKE
MONTREAL, QUÉBEC,
CANADA H1X 2B2

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ARMORACIA LACUSTRIS (BRASSICACEAE) REDISCOVERED IN OHIO

JAMES S. MCCORMAC

Key Words: *Armoracia lacustris,* rediscovery, ecology, Ohio

Armoracia lacustris (A. Gray) Al-Shehbaz & V. Bates (Lake Cress) is a heterophyllous mustard of aquatic habitats which occurs over an extensive area in eastern North America, ranging from Pennsylvania and Virginia west to the 95th meridian, south to Florida and Texas, and north to southern Canada. Within this broad distribution, *A. lacustris* is irregularly dispersed, and has been reported from widely scattered localities in nineteen states and two provinces. It has been proposed as a candidate for listing as federally endangered or threatened (Federal Register, 1990) due to its apparent rarity. This taxon has a confusing nomenclatural history, having been placed in six different genera. In recent years the name *Armoracia aquatica* (Eaton) Wieg. had been widely used for Lake Cress, but Al-Shehbaz and Bates (1987) demonstrated that this name is invalid, and proposed the new combination *Armoracia lacustris* (A. Gray) Al-Shehbaz & V. Bates.

Lake Cress was last collected in Ohio on 10 June 1936 by Floyd Bartley near Circleville, Pickaway County (Cooperrider, 1982). There have been no reports of this plant in Ohio since that time; as of 1990 it was listed as presumed extirpated by the Ohio Department of Natural Resources (Div. of Natural Areas and Preserves, 1990). Historical locations, almost all of which date from the late nineteenth century, are known from eight Ohio counties (Coshocton, Erie, Licking, Lorain, Lucas, Madison, Perry, Pickaway) based on surveys of CLM, GH, KE, MICH, MU, NY, OS, and PH. Published county dot maps of *Armoracia lacustris* in Ohio by Al-Shehbaz and Bates (1987) and Easterly (1964) included Clark County and omitted Perry County. I could not locate a specimen to substantiate the Clark County report, and OS contains an 1895 collection from Perry County.

On 19 June 1991, M. A. Moser, Jr., S. J. Stine and I were conducting field investigations of riparian habitats along St. Marys River in west-central Ohio. In an Ash-Maple floodplain woods in Mercer County, we located a population of *Armoracia lacustris* which contained ca. 180 fertile plants and numerous sterile rosettes. The plants were growing in wet soil of a seasonally inun-

dated, diassociated channel of the river, and were flowering and fruiting vigorously.

St. Marys River is a moderately large stream of low gradient (2.9′ per mile) (Div. of Water, 1960) which originates in western Auglaize County, Ohio and flows west and north to its confluence with the Maumee River, a major drainage of the Lake Erie basin. In Ohio, the St. Marys is characterized by a broad, well-forested floodplain with numerous oxbows and buttonbush swamps; it is one of the few remaining unchannelized rivers in western Ohio. Near Fort Wayne, Indiana, a low-lying divide known as the Maumee Terrace separates the St. Marys and Wabash drainages (Thornbury, 1958). During periods of extreme flooding, waters from the St. Marys drainage unite with the Mississippian drainage of the Wabash River through this divide (Greene, 1935), thus representing a potential migratory corridor for plants between the Mississippi River and Lake Erie drainages. *Armoracia lacustris* has been collected at several locations in the Wabash system in central and eastern Indiana (Deam, 1940).

Additional field surveys of the St. Marys River area during June and July by Moser and myself located a total of six separate populations of *Armoracia lacustris* (Figure 1), distributed in all three Ohio counties through which the St. Marys flows (Auglaize, Mercer, Van Wert). These populations range in size from ca. two dozen plants to 1000+ plants scattered over two to three acres at a site in Mercer County. All populations occur in old river channels now isolated from the St. Marys except during periods of flooding, when they are temporarily inundated. The oxbows in which *A. lacustris* grows are in semi-open riparian woodlands dominated by *Acer saccharinum* L. and *Fraxinus pennsylvanica* Marsh.; *Cephalanthus occidentalis* L. is always present in the wettest sections of these oxbows. Typical herbaceous associates include *Carex crus-corvi* Shuttlew., *C. lupulina* Muhl., *C. muskingumensis* Schwein., *C. tribuloides* Wahlenb., *Leersia lenticularis* Michx., *L. oryzoides* (L.) Swartz, *Ludwigia palustris* (L.) Ell., *Polygonum hydropiperoides* Michx., *Proserpinaca palustris* L., *Rorippa sessiliflora* (Nutt.) Hitchc., *Samolus floribundus* HBK., and *Saururus cernuus* L.

By mid-June, surface water was no longer present in the oxbow habitat, and *Armoracia lacustris* was growing in a soft, thick, muddy substrate in a loosely defined zone along the periphery of

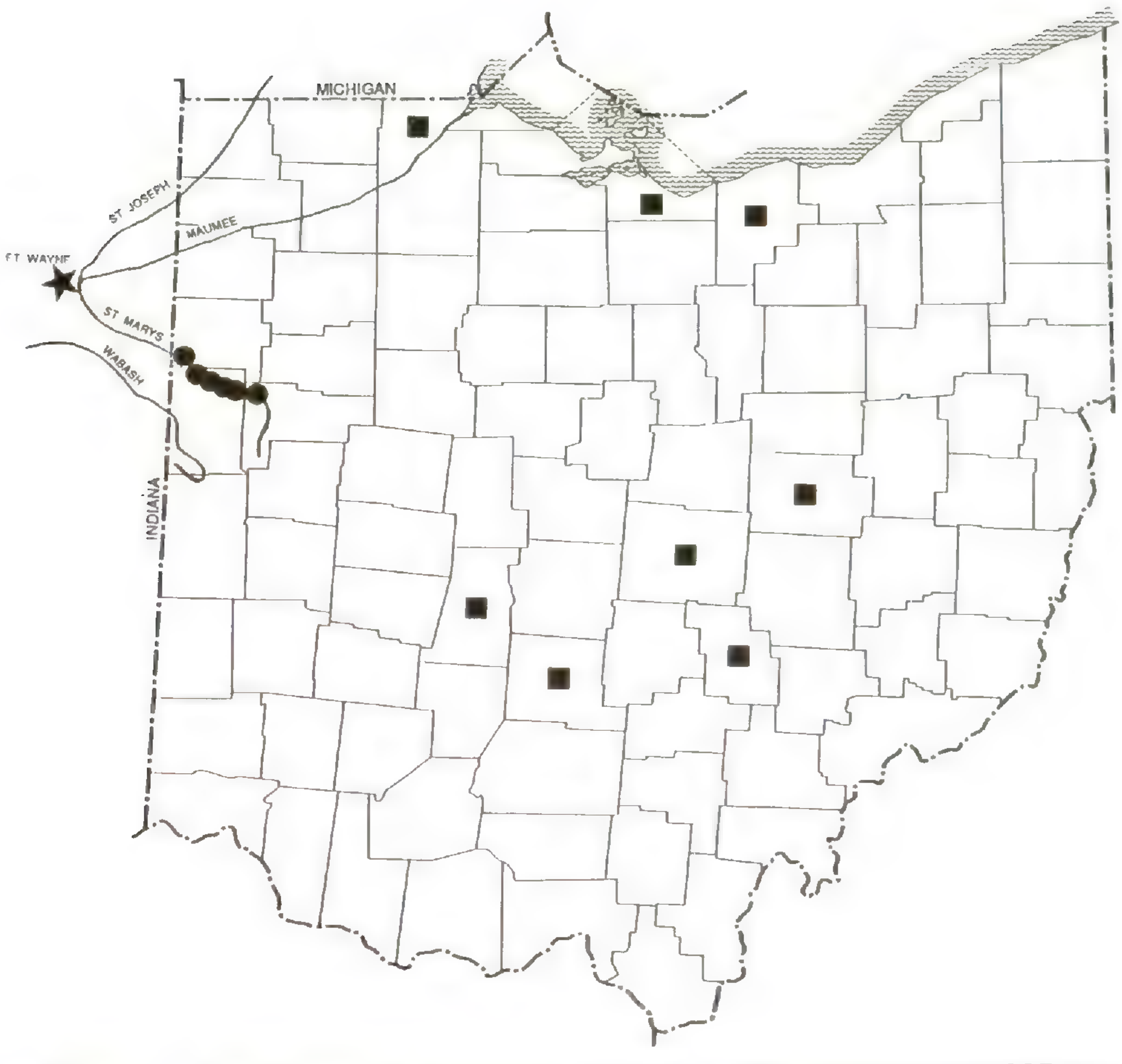

Figure 1. Distribution of *Armoracia lacustris* in Ohio showing pre-1937 records (■), and 1991 collection sites (●).

each oxbow. Sterile rosettes greatly outnumbered flowering and fruiting plants in all populations. Few mature seeds could be found by random examination of apparently well-developed fruits; reproduction in these populations was mostly, if not entirely, by vegetative means. Cauline leaves easily detach from the plants; soon after falling onto the soft muck, they send out roots and eventually form rosettes. LaRue (1942) described this method of regeneration in detail; leaves I collected and placed on moist potting soil also rooted and formed rosettes. The percentage of these rosettes which survive and develop into mature plants in the wild is not known.

Voucher specimens of *Armoracia lacustris* collected in this study are deposited in CLM, GH, KE, MICH, MU, NY, OS and PH.

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OHIO DEPARTMENT OF NATURAL RESOURCES
DIVISION OF NATURAL AREAS AND PRESERVES
1889 FOUNTAIN SQUARE, BLDG. F
COLUMBUS, OH 43224

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NEW ENGLAND NOTE

UTRICULARIA INFLATA WALTER (LENTIBULARIACEAE) IN MASSACHUSETTS

BRUCE A. SORRIE

On 11 October 1990, I traveled to Federal Pond, on the border of Carver and Plymouth in Plymouth County, Massachusetts to verify a report of black spruce, *Picea mariana* (Miller) BSP. According to Austin Mason, Regional Forester with the state Division of Forests and Parks, a small stand of this spruce occurred on the east shore of the pond. If verified, it would represent only the second extant population of *P. mariana* in southeastern Massachusetts. After a short search, four small trees were found in deep peat at the edge of a cove just within the boundary of Plymouth, but none elsewhere, including several peat islands offshore.

Of even more interest, however, were a few flowering bladderworts in another cove that obviously were related to *Utricularia radiata* Small, a common species in acid lakes and ponds in Massachusetts, but which were much larger. The scape of one measured 23 cm and the floats spanned 18 cm! Particularly distinct, in comparison to specimens of *U. radiata,* were the very large flowers, long floats that tapered to the axis, thick peduncle and stem, and massive system of bladder-bearing branches. These plants keyed easily in Godfrey and Wooten (1981) and Schnell (1976) to *U. inflata* Walter, a species heretofore unknown north of southern New Jersey. A return visit on 20 October found *U. inflata* abundant around much of Federal Pond, especially in the lee of peat islands. Associates included *Utricularia purpurea* Walter, *Nymphaea odorata* Aiton, *Myriophyllum heterophyllum* Michaux, *M. humile* (Raf.) Morong, *Lobelia dortmanna* L., *Juncus militaris* Bigelow, and *Scirpus subterminalis* Torrey. Specimens (*BAS 5317* and *5332*) have been deposited at GH, MASS and in my personal herbarium.

This discovery marks the 13th *Utricularia* for Massachusetts and New England. As with other disjunctions, one must consider the possibility of human-aided introduction, particularly in this case since Federal Pond is used as a reservoir for a cranberry growing firm. Mr. David Parks of the Federal Furnace Cranberry Company assured me that although New Jersey and Massachu-

setts have extensive cranberry cultivation, there is no movement of plant material or soil between the states; rarely a piece of machinery may be transported. Griffith (1913) stated that Federal Pond was created in 1793 by damming Crane Brook, in order to mine bog iron. Certainly there has been ample time since then for propagules to be transported, most likely via waterfowl or herons. One might argue that since there are hundreds of ponds in southeastern Massachusetts, *U. inflata* should be widespread. However, there are dozens of rare species that defy such logic, occurring in but a tiny fraction of the apparently suitable habitat in the Plymouth/Cape Cod area. Such is true of some of the other inhabitants of Federal Pond: *Carex lanuginosa* Michaux (here at its sole southeastern Massachusetts site), *Carex striata* Michaux (formerly *C. walteriana* Bailey), red-bellied turtle (*Chrysemys rubriventris*), and the black spruce.

ACKNOWLEDGMENTS

Access to Federal Pond, and a pair of oars, was generously provided by the Federal Furnace Cranberry Company of Carver, MA. A boat was provided by the MA Division of Fisheries and Wildlife. Field assistance was ably provided by Ann Buckley, Ted Hendrickson, and Chuck Katuska. The staff of GH is thanked for access to their holdings and library resources. Inventory was performed when I was Botanist for the Massachusetts Natural Heritage and Endangered Species Program.

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202 HOLLY PINES DRIVE
PINEHURST, NC 28374

RHODORA, Vol. 94, No. 880, pp. 393–394, 1992

BOOK REVIEW

MacKinnon, A., J. Pojar and R. Coupe, Eds. 1992. *Plants of Northern British Columbia.* 344 pp. British Columbia Ministry of Forests and Lone Pine Publishing, 206, 10426-81 Ave., Edmonton, Alberta, Canada T6E 1X5. ISBN 1-55105-015-3. (Price: $19.95 Canadian, paper).

This outstanding book is the only field guide to the plants of northern interior British Columbia and, to my mind, the best available field guide for the interior of Alaska. As a field guide, it is limited to the more common plants, but includes trees, shrubs, graminoids, ferns and bryophytes in addition to the showy herbaceous angiosperms generally covered in such guides. Approximately 550 species are illustrated, but the book enables the user to identify at least fifty additional species. Forty species and subspecies of willow are described!

The book is organized by family, and emphasizes the Ericaceae, Salicaceae, Rosaceae, Liliaceae, Asteraceae, Scrophulariaceae, Fabaceae, Ranunculaceae, Orchidaceae and Saxifragaceae, although common members of other families are included. A table of contents directs the user to the family, to keys, and to conspectuses. For each species, the authors provide clear descriptions of habit, leaves, flowers, fruits and ecology. Notes discuss characters that distinguish similar species, and provide ethnobotanical information. Each species is illustrated with color photographs of flowers and/or fruits, and with line drawings showing habit, leaves or fruits. The line drawings of trees and shrubs are charmingly illustrated with an appropriate mammal for scale. There are some errors, notably the transposition of photos for several species of graminoids and incorrect illustrations for three lichens, for which the publisher has provided a page of errata.

Several unique features make this an exceptionally user-friendly field guide. Difficult groups of plants are provided with easy-to-use, clear dichotomous keys (trees, *Ribes,* genera of the Asteraceae, Orchidaceae, *Arnica, Platanthera, Pedicularis, Salix*). An outstanding picture-key to the grass genera makes identification relatively simple. In addition, species in large and difficult groups (*Ribes, Vaccinium, Potentilla, Viola, Pedicularis,* Liliaceae) are distinguished in a "conspectus"—a two-page table allowing the user to directly compare the stems, leaves, flowers, or habitat of

up to fifteen species. This table is especially useful in large groups where space has not permitted the authors to provide illustrations or complete descriptions for all species. The authors frequently use leaf silhouettes in keys and comparative tables where these aid identification (Fabaceae, *Petasites, Potentilla,* Ranunculaceae), and have augmented the key to *Salix* with leaf photocopies showing venation as well as outline.

This little book is, without a doubt, the most usable and most complete field guide I have encountered. It enables the amateur or professional to easily identify almost any vascular or nonvascular plant encountered—even sedges. The excellent illustrations, use of leaf silhouettes, and the innovative "conspectus" for large genera simplifies identification dramatically. I highly recommend this book for anyone planning travel to British Columbia, the Yukon, Mackenzie District, or to Alaska, as well as to anyone planning to write a field guide.

LISA A. STANDLEY
VANASSE HANGEN BRUSTIN, INC.
101 WALNUT STREET, P.O. BOX 9151
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RHODORA, Vol. 94, No. 880, p. 395, 1992

IN MEMORIAM

William Holland Drury
1921–1992

William Holland Drury, Professor at The College of the Atlantic in Bar Harbor, Maine, died on March 26, 1992. Born in Newport, RI, he was a 1942 magna cum laude graduate of Harvard College. He served with the United States Navy from 1942 until 1945, serving tours of duty both in the North Atlantic and the South Pacific. He returned to graduate study at Harvard after the war and was awarded his doctorate in biology and geology in 1952.

Dr. Drury was a member of the New England Botanical Club for forty-five years, first joining in 1947. He was elected to serve as Vice-president from 1962–65, and as President from 1965–68.

One of the country's best ecologists, Dr. Drury, among other accomplishments, showed, along with his co-worker Dr. Ian Nisbet, that the ideas of ecological succession found in most ecology textbooks are based upon wishful thinking, rather than on observed facts. He taught ecology and evolutionary biology at Harvard for many years. He was an active member of the Massachusetts Audubon Society, and served as its Director of Education and Research from 1972 to 1976. The esteem in which Dr. Drury was held by some individuals who knew him is largely the reason that Massachusetts Audubon today occupies Drumlin Farm, which was donated to the Society to help further his research on birds and ecology. He traveled widely, and was learned about many subjects, one of which was the flora of Alaska.

An active conservationist, Dr. Drury helped sound the early alarms about pesticides and other environmental insults. He served as a member of the President's Science Advisory Council during both the Kennedy and Nixon administrations. He was instrumental in reintroducing the peregrine falcon to the Northeast, and had recently spent much time on studying and enhancing diversity among shorebird populations around the Gulf of Maine.

In 1976, Dr. Drury joined The College of the Atlantic, where he was a teacher, researcher, and director of advanced studies until shortly before his death. He was proud of his role there, which he summarized to me as, "Whatever else we do for students, we certainly teach them how to think."—[Norton H. Nickerson]

RHODORA, Vol. 94, No. 880, p. 396, 1992

IN MEMORIAM

Herman Royden Sweet
1911–1991

Dr. Herman R. Sweet died on October 2, 1991, at his home in Florida, shortly after completing a journey in which he visited the Boston area. A memorial service in his honor was held at Goddard Chapel, Tufts University, Medford in early November. Interment was in Mount Auburn Cemetery, Cambridge.

Volume 92 of RHODORA was dedicated to Dr. Sweet on the occasion of his retirement from service to the New England Botanical Club; he served as its Treasurer for twenty-three years, and had been a member since 1959. An account of his many activities and duties for the Club, for Tufts University where he was a long-time faculty member, and for the American Orchid Society of which he was an active member, may be found in the frontispiece of RHODORA, Vol. 92, (No. 869, January, 1990). —[Norton H. Nickerson]

NEBC AWARD FOR THE SUPPORT OF BOTANICAL RESEARCH

The New England Botanical Club will offer an award of $1000 in support of botanical research to be conducted in relation to the New England flora during 1993. This award is made to stimulate and encourage botanical research on the New England flora, and to make possible visits to the New England region by those who would not otherwise be able to do so. The award will be given to the graduate student submitting the best research proposal dealing with field studies in systematic botany, biosystematics, plant ecology, or plant conservation biology, although proposals for research in other areas of botany will also be considered. This award is not limited to graduate students at New England institutions, nor to members of the New England Botanical Club. Papers based on this research must acknowledge the NEBC's support, and it is encouraged that they be submitted to RHODORA for possible publication subject to standard review processes.

The 1992 New England Botanical Club Award for the Support of Botanical Research was awarded to Mr. Francois Lutzoni, a graduate student at Duke University, in support of his Ph.D. research, entitled "Phylogenetics of *Omphalina* (Basidiomycotina, Agaricales) and the Evolution of Lichenization."

Applicants should submit a proposal of no more than three double-spaced pages, a budget (the budget will not affect the amount of the award), and a curriculum vitae. Three copies of the application must be submitted. Two letters in support of the proposed research, one from the student's thesis advisor, are also required. Proposals and supporting letters must be received no later than March 1, 1993. The recipient of the award will be notified by April 30, 1993. Proposals should be sent to:

Awards Committee
The New England Botanical Club
22 Divinity Ave.
Cambridge, MA 02138

U.S. NATIONAL ARBORETUM HERBARIUM

The Herbarium of the U.S. National Arboretum (NA), Washington, DC announces the installation of a new Spacesaver compactor filing system. The project, to be installed in three modules, was started in January, 1992 and should be finished in July, 1992. The transfer of the herbarium specimens will take place at the completion of each of the three modules, with the transfer of specimens into the final module to be completed in late 1992. When the shift of the specimens is completed, scientists and students will be welcome to visit and use the new system.

The National Arboretum herbarium collection of over 600,000 specimens concentrates on extant and potential economic plants from indigenous and cultivated sources on a world-wide basis. The collection is especially rich in woody landscape plants—species, cultivars and clones—cultivated in the United States.

Major genera include: *Amaranthus, Salix, Ilex, Viburnum, Pyracantha, Coffea, Trifolium, Medicago, Magnolia,* among many other agricultural and nursery crop plants. Major geographical areas represented by collections of wild-occurring and cultivated plants include: North America, Japan, the Peruvian Andes, Tierra del Fuego (Argentina), Juan Fernandez Islands (Chile), The People's Republic of China, and The Republic of Korea. Large portions of the Isaac C. Martindale Herbarium (PHIL) a 19th century world-wide collection, were acquired in 1964. Sizable sections of the Catholic University Herbarium (LCU) and the Morris Arboretum Herbarium (MOAR) were incorporated into NA in 1984.

The National Arboretum Herbarium welcomes **exchange** of herbarium specimens of economic plants and their wild-occurring relatives—landscape, food, forage, commercial, industrial, weed, etc.—both indigenous and cultivated. The herbarium is also pleased to send material world-wide on **loan** for study by specialists in various groups.

Dr. T. R. Dudley became Lead Scientist in charge of the Herbarium and the taxonomic and nomenclatural research unit at the National Arboretum, effective 1 October 1991. Mr. P. M. Mazzeo, Botanist, is responsible for herbarium curatorial activities. Dr. Frederick G. Meyer, formerly Botanist in charge of the Herbarium, retired effective 30 September 1991.

Contact either Dr. T. R. Dudley or Mr. P. M. Mazzeo for exchanges and loans:

U.S. National Arboretum Herbarium
3501 New York Avenue, NE
Washington, DC 20002-1958, U.S.A.

Dr. Dudley's phone: 202-475-4842
Mr. Mazzeo's phone: 202-475-4841
FAX: 202-475-5694

THE 1992 JESSE M. GREENMAN AWARD

The 1992 Jesse M. Greenman Award has been won by Sharon Elaine Bartholomew-Began for her publication "A morphogenetic re-evaluation of *Haplomitrium* Nees (Hepatophyta)," published as Volume 41 of Bryophytarum Bibliotheca. This study is based on a Ph.D. dissertation from Southern Illinois University at Carbondale, under the direction of Dr. Barbara Crandall-Stotler.

The Greenman Award, a certificate and a cash prize of $500, is presented each year by the Missouri Botanical Garden. It recognizes the paper judged best in vascular plant or bryophyte systematics based on a doctoral dissertation published during the previous year. Papers published during 1992 are now being accepted for the 25th annual award, which will be presented in the summer of 1993. Reprints of such papers should be sent to:

Dr. P. Mick Richardson
Greenman Award Committee
Missouri Botanical Garden
P.O. Box 299
St. Louis, MO 63166-0299, U.S.A.

In order to be considered for the 1993 award, reprints must be received by 1 June 1993.

RHODORA, Vol. 94, No. 880, p. 400, 1992

REVIEWERS OF MANUSCRIPTS
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RHODORA

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